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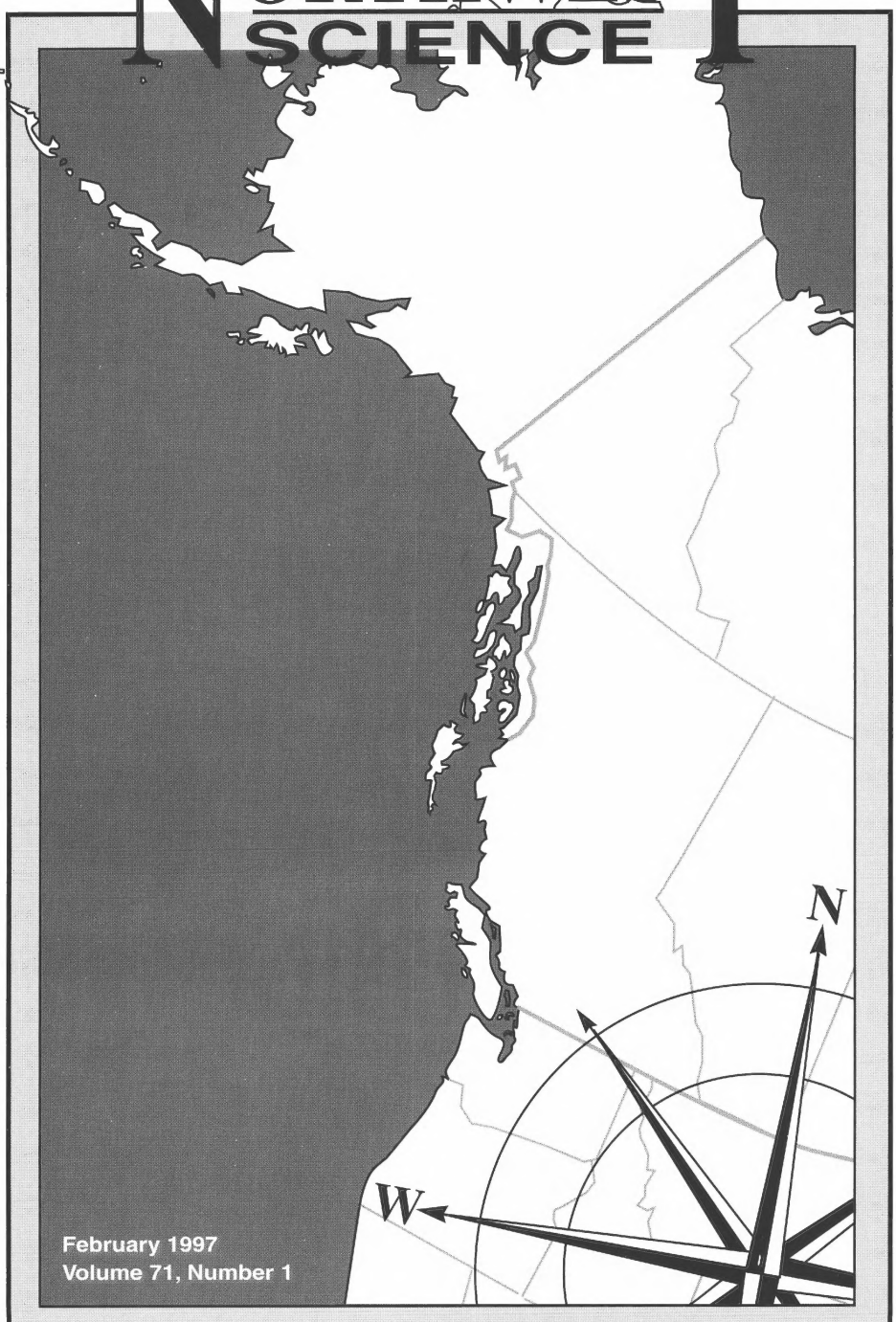

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1997 Annual Meeting

The 70th annual meeting of the Northwest Scientific Association will be hosted by Eastern Washington University and held at the new Riverpoint Campus in Spokane, Washington. The meetings will be held jointly with the Lichen Guild and the Society for Experimental Biology and Medicine on March 26-28, 1997. Following a business meeting for the Board of Trustees on March 26, scientific sessions will occur on the following two days with a variety of concurrent sections and symposia. There will be symposia on wildlife refuge research and management issues, archaeological studies in the Northwest, and Inland Northwest biotechnology. Field trips will focus on various aspects of the natural history of Turnbull Wildlife Refuge.

Both members and non-members of the Northwest Scientific Association are welcome at the meetings, and students are especially encouraged to attend. Information on all aspects of the 70th annual meeting (including accommodations and section and symposium topics) will be available and constantly updated at: http://www.csmt.ewu.edu/csmt/nwsci/nwsci.htm.

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Coyote (*Canis latrans*) Food Habits in Three Urban Habitat Types of Western Washington

Abstract

The coyote (*Canis latrans*) is a common resident in urban areas throughout the United States, yet little is known about coyote diets in these environments. I characterized the annual diet of coyotes in an urban environment of western Washington by analyzing their scat from three areas representing typical patterns of human occupation and density: residential (1413 humans/km^2), mixed agricultural-residential (348 humans/km^2), and mixed forest-residential (126 humans/km^2). Coyote scats were collected twice a month for 1 year (Nov. 1989-Oct. 1990) in each habitat type. Fruits and mammals were the largest classes of food items in all habitat types and their seasonal use was similar among habitats. Apple (*Malus* spp.) and cherry (*Prunus* spp.) were the most abundant fruits in the scats, and ranged from 22-41% and 9-13% of the annual diet, respectively. Vole (*Microtus* spp.) was the most abundant mammalian food item (41.7%) of coyotes in mixed agricultural-residential habitat while house cat (*Felis catus*) and squirrel (*Sciurus* spp. and *Tamiasciurus* spp.) were the two most abundant mammalian food items (13.1 and 7.8%, respectively) of coyotes in residential habitat. No single mammalian species made up >6.0% of the coyote diet in mixed forest-residential habitat. Coyotes in my western Washington study area rely on foods that result from human activity but those foods, particularly mammals, may change as land use patterns change.

Introduction

Coyotes (*Canis latrans*) are becoming increasingly common in human modified habitats throughout North America (Atkinson and Shackleton 1991, MacCracken 1982). One possible explanation for this trend is that human-dominated areas produce abundant food sources for coyotes. Coyotes living in urban habitats have relatively small home ranges (Atkinson and Shackleton 1991, Shargo 1988), which may indicate abundant food resources. However, little is known about the diet of coyotes in these areas. MacCracken's (1982) description of the annual diet of coyotes in residential habitat was based on a small number of scats (n = 97) collected during a single month. Atkinson and Shackleton (1991) described the diet of coyotes in an area that was mostly agricultural (>50% of the study area) and Shargo's (1988) description of urban coyote diet was based on 22 scats. Additionally, none of these studies looked at diet as a function of human density.

Coyotes may play an important role in human modified landscapes. Soulé et al. (1988) suggested that coyotes may reduce the abundance of house cats (*Felis catus*) and other small mammalian carnivores that prey on song birds and thus indirectly contribute to the maintenance of native avifauna. My objectives were to document the annual diet of coyotes in three types of urban habitat of western Washington and to qualitatively assess how coyote diets changed as a function of land use patterns and human density.

Study Area

The study area, located in the low elevation (<200 m) region of King and Snohomish counties, was bordered on the west by Puget Sound and on the east by foothills of the Cascade Mountains. This portion of Washington lies in the wetter region of the Western Hemlock Zone (Franklin and Dyrness 1984). The study area was logged at the turn of the 19th century. Much of the land has been developed for urban and agricultural uses but there are numerous patches of 40-80 year-old naturally regenerated forest dominated by Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), western red cedar (*Thuja plicata*), red alder (*Alnus rubra*), and maple (*Acer* spp; Franklin and Dyrness 1984).

Urban areas are mosaics of habitat patches differing in size and intensity of human use. I chose

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three habitat types in which to establish permanent scat collection routes (hereafter routes): residential habitat, mixed agricultural-residential (hereafter mixed agricultural) habitat, and mixed forest-residential (hereafter mixed forest) habitat. I described coyote diets in these habitats, which represented the typical range of different land uses in urban western Washington. I characterized habitat types on the basis of human density (Census Population and Housing 1990, Seattle, Wash., unpubl. data). I calculated the density of humans within census tracts in which the route was located and census tracts which were within 1 km of a route. I included density figures from census tracks within 1 km of routes to help characterize the area from which coyotes likely would have foraged. Despite efforts to characterize collection areas, coyotes may have deposited scats in habitats very different from where they foraged. Census tracts are areas of similar land use and human density patterns for which human demographic statistics are calculated (Census Population and Housing 1990, Seattle, Wash., unpubl. data).

Residential habitat, which was predominantly single family housing development, represented the most urbanized edge of the coyote's range in King County (Quinn 1991) with a mean density of 1412.72 (SE = 260.12) humans/km^2. Coyotes in this habitat type were closely associated with remnant patches of second growth forest found in parks and riparian areas (Quinn 1995). Mixed agricultural habitat had a density of 347.97 (SE = 51.52) humans/km^2 and was predominantly pasture land supporting dairy farms. Mixed forest habitat had a density of 125.66 (SE = 17.74) humans/km^2 and was predominantly second growth forest with interspersed single family housing developments.

To minimize the chance of encountering scats from midsized carnivores other than coyotes, I located routes in regions of relatively high coyote density (Quinn 1992, 1995), outside the range of the indigenous red fox (*Vulpes vulpes cascadensis,* Aubry 1984), and in areas where bobcats (*Felis rufus*) and introduced red fox (*Vulpes vulpes*) were extremely rare (D. A. Ware, Wash. Dept. Wildl. unpubl. data; J. R. Consolini, Wash. State Trappers Assoc., pers. comm.). There was no evidence of feral dogs (*Canis familiaris*) near any of the routes based on personal records of an animal damage control trapper who has worked in these areas for the past three years (J. R. Consolini, Wash. State Trappers Assoc., pers. comm.). My field observations were consistent with these assumptions.

Methods and Materials

I cleared all scats from routes, which consisted of unpaved trails, in October 1989. From November 1989 through October 1990, I collected all scats at 2-week intervals from each route. Routes were 5-9 km in total length but were discontinuous because of the patchy nature of coyote habitat and suitable scat collection areas. The residential route was composed of 6 segments, totaling 9 km in length, and located near the northern border of Seattle. All segments were within 0.5-8.0 km of each other and were in patches of second growth forest surrounded by residential housing developments. The mixed agricultural route, totaling 5 km in length, was composed of 3 segments separated from each other by 0.3-0.5 km. This route was located 5 km north of Redmond in the Sammamish River flood plain. The flood plain was predominantly pasture land surrounding small farms. The adjacent uplands consisted of housing developments and patches of second growth forest. The mixed forest route was 5 km in length and located on Novelty Hill 12 km northeast of Redmond. This route was composed of 2 segments separated by approximately 0.5 km along a power line right-of-way off Novelty Hill road. Except for blackberry (*Rubus* spp.) and grasses directly below the power lines, the area was predominantly second growth forest with interspersed housing developments.

I identified scats by their physical appearance, including size (Danner and Dodd 1982) and shape (Murie 1954). As an added safeguard against including dog scats in the samples I assumed that scats composed of >50% commercial dog food (estimated visually) originated from dog. Commercial dog food was easily identified under low magnification by the abundance of grain particles.

Collected scats were individually bagged and dried at 50°C for 48 hours. Food items in dried feces were separated manually and identified by comparison with reference collections of mammal skeletons and guard hairs, and with hair medulla (Moore et al. 1974) and plant seed keys (Martin 1961).

I used Knowlton's (1964) method for estimating coyote diet because it produces an easily understood qualitative measure of food importance. I visually estimated the volume of each individual food item to the nearest 5% of each scat. I counted only the major food item (>40% by volume) of each fecal specimen (Andelt 1985, Knowlton 1964). When two items each composed >40% of fecal volume, I assigned a 0.5 count to each.

Because I did not sample from replicate habitat types, I made only qualitative comparisons among habitat types. I defined seasons as: spring (1 Apr.-30 Jun.), summer (1 Jul.-30 Sep.), fall (1 Oct.-31 Dec.), and winter (1 Jan.-31 Mar.).

Results

I collected a total of 1435 coyote scats from all habitat types (735 from residential, 449 from mixed agricultural, and 251 from mixed forest). From 88 to 91% of scats from each habitat consisted of a single food item as defined in the methods. Fruits and mammals were the two most abundant classes of food items in scats from all habitats (Table 1). Apple (*Malus* spp.), cherry and plum (*Prunus* spp.), vole (predominantly *Microtus*), and house cat each comprised >10% of the diet in one or more habitat types. Bird, reptile, insect, livestock, and vegetation other than fruit were minor components (<3%) of the diet in each habitat type (Table 1).

Coyotes in mixed agricultural habitat had the highest proportion of mammals in the diet followed by the residential habitat (Table 1). Vole was the most abundant mammalian food item in the diet of coyotes in mixed agricultural habitat. Cat was the most abundant mammalian food item (13.1%) in residential habitat followed by squirrel (*Sciurus* spp. and *Tamiasciurus* spp.) at 7.9% of the annual diet. With the exception of muskrat (*Ondatra zibethica*), which was not found in scats from residential habitat, and dog, coyote, and raccoon (*Procyon lotor*), which were found only in scats from residential diets, diets in all habitat types contained the same mammal species. Muskrat, dog, coyote and raccoon each made up <3.0% of the diet in each habitat. Mammals made up the majority of the spring diet (>58.0%) in all habitat types. For the remainder of the year, mammals were a fairly consistent proportion of the diet (approx. 30.0%) except in the mixed agricultural habitat. During winter, coyote diets in mixed agricultural habitat contained twice as much mammal as in other habitat types (Figure 1).

TABLE 1. Food items, by percent, in the annual diet (1989-90) of western Washington coyotes (*Canis latrans*) from residential habitat, mixed agricultural - residential habitat (mixed agric), mixed forest - residential habitat (mixed forest), and all habitats combined (pooled).

	Habitat Type			
Food Item	Residential	Mixed Agric	Mixed Forest	Pooled
Fruit				
Apple (*Malus* spp.)	29.4	21.7	40.6	29.1
Cherry (*Prunus* spp.)	9.7	12.8	9.4	10.6
Other/unknown	3.5	2.7	7.0	3.9
Total fruit	42.6	37.2	57.0	43.6
Mammal				
Vole (*Microtus* spp.)	3.3	41.7	5.7	15.9
Squirrel (*Sciurus*/ *Tamiasciurus* spp.)	7.9	1.4	1.1	4.6
Cat (*Felis catus*)	13.1	2.3	3.3	7.8
Mountain beaver (*Aplodontia rufa*)	3.9	0.5	5.4	3.1
Other	7.8	8.3	12.8	8.9
Unknown	2.3	0.8	3.6	2.1
Total mammal	38.3	55.0	31.9	42.4
Miscellaneous				
Bird/reptile	2.7	1.6	2.8	2.4
Grass/other vegetation	4.0	2.3	3.4	3.4
Garbage	1.4	1.1	1.4	1.3
Dogfood	4.5	1.8	1.5	3.1
Unknown	6.4	1.1	2.0	3.9

Coyotes in mixed forest habitat had the highest proportion of fruits in the diet followed by coyotes in residential habitat (Table 1). Cherry and plum were the first dietary fruits to appear in the summer followed by berry (*Rubus* spp.). Apple, the most abundant dietary fruit in all habitat types (Table 1), generally did not appear in the diet until the fall but remained an important food item into the winter. The greatest proportion of dietary fruits occurred in the summer or fall in all habitat types (Figure 1). The higher annual proportion of fruits in mixed forest habitat was primarily the result of high winter consumption of fruits in that habitat type (Figure 1).

Discussion

The diets of coyotes in all three habitat types were similar in composition for the major food classes (mammals and fruits). Coyotes in all habitat types took advantage of the seasonal availability of mammals and fruits. The winter/spring peak of mammals

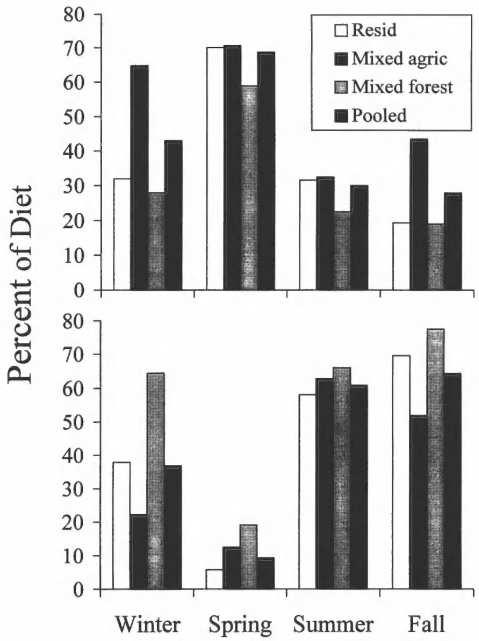

Figure 1. Percentages of mammals (top panel) and fruits (lower panel) in the seasonal diet of coyotes from three habitat types in western Washington, 1989-90: residential habitat (resid), mixed agricultural-residential habitat (mixed agric), mixed forest-residential habitat (mixed forest), and all habitats combined (pooled). I defined seasons as winter (1 Jan.-31 Mar.), spring (1 Apr.-30 Jun.), summer (1 Jul.-30 Sep.), and fall (1 Oct.-31 Dec.).

in the diet corresponded to the time when the availability of fruits was probably at its annual low. Fruits became an important class of coyote food in June and remained important until January. This study was consistent with other studies that have shown fruits to be important dietary components in many coyote populations throughout North America (Dibello et al. 1990, MacCracken 1982, Toweill and Anthony 1988). Apple was the most important fruit in the diet of coyotes in my study area because it was available at times of the year when mammals and other fruits were relatively scarce. Apple ripens later in the year than other fruits and cooler fall and winter temperatures slow the decomposition of apples and make them available for relatively longer periods. Although fruit was a major component of the coyote diets in this study, its importance may be overestimated. Diets containing large quantities of fruit may increase the rate of scat deposition (Andelt and Andelt 1984). In addition, conclusions about dietary preference or the importance of particular food items to coyote fitness should be made cautiously because coyote diet was not assessed in terms of food item availability.

While mammals were important components of the diet in all habitat types, there was considerable variation in proportions of individual mammal species. Coyotes in mixed forest habitat had the lowest proportion of mammals in the diet and no single species of mammal made up >6% of the annual diet. Voles dominated the mammalian portion of coyote diets in the mixed agricultural habitat. This is consistent with Atkinson and Shackleton's (1991) study of coyote food habits in a predominantly agricultural habitat in Canada where voles made up nearly 70% (by volume) of the coyote diet. Cat was the most abundant mammalian food item for coyotes in the residential habitats. In 1991, the Humane Society of the United States (R. Lamb, Humane Soc. of the U.S., pers. comm.) estimated that there were approximately one cat per three households in the U.S. Clearly, cats represent an abundant resource for predators such as the coyote, particularly in areas with high human density. Shargo (1988) found 13.6% occurrence of cat in 22 scats collected in his urban study area, which was most similar to my residential habitat type. However, cat was absent and only a minor food item (<3% frequency of occurrence) of urban/rural coyotes in British Columbia (Atkinson and Shackleton 1991) and urban coyotes in California (MacCracken 1982), respectively.

One major consequence of human activity is the creation of food sources that are readily exploited by coyotes (Gier 1975). Human alteration, particularly logging and the clearing of land for agriculture, may have facilitated the colonization of Oregon, Washington, and British Columbia by coyotes (Dalquest 1948). In western Oregon, many important food items of coyotes were associated with clear-cut areas rather than the surrounding forest (Toweill and Anthony 1988). In British Columbia, coyotes fed primarily (>70% by volume) on meadow voles (*Microtus* spp.) living in agricultural lands that were previously forested (Atkinson and Shackleton 1991). My study suggested that coyotes in western Washington eat large

quantities of food that result from human activity and that coyote diet may change as a function of human density and land-use.

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Long-Term Influence of Glyphosate Herbicide on Demography and Diversity of Small Mammal Communities in Coastal Coniferous Forest

Abstract

This study tested the hypothesis that (1) abundance and related demographic parameters of small mammal populations, and (2) species diversity of small mammal communities, would be adversely affected in herbicide-treated habitats at 9 and 11 years after treatment in coastal coniferous forest. Study areas were located in south-coastal British Columbia, Canada, in the Coastal Western Hemlock (CWH_{dm}) biogeoclimatic zone where small mammal populations were intensively sampled on paired control and treatment sites. Average density of deer mice (*Peromyscus maniculatus*) during summer periods (1981-1990) was lower in the treatment than control in the immediate post-treatment (PT) period (1982), with comparable numbers in 1983, 1985, and 1990. At the 11-year PT area, deer mouse numbers were similar on control and treatment sites in 1978, 1979, 1980, and 1990. Average density of Oregon voles (*Microtus oregoni*) was higher on treatment than control sites at 9 and 11 years after treatment. Townsend chipmunks (*Eutamias townsendii*) tended to be less abundant on the treatment than control site 9 years PT but were essentially absent from the 11-year PT study area. There was no difference in average density of shrew (*Sorex* spp.) populations between control and treatment sites at either study area. It is likely that post-harvest successional change has more of an impact on small mammal abundance than change induced by a herbicide treatment. Our results suggest that glyphosate herbicide did not adversely affect reproduction, survival, or growth of deer mice and Oregon voles in coastal forest a decade after application. Species richness and diversity of small mammal communities changed little over the decade following treatment. This study is the first investigation on the effects of forest herbicide use on demography and diversity of small mammal communities that extends to a decade.

Introduction

Vegetation management is an important part of forest renewal in the temperate coniferous forests of North America. Silviculture programs must deal with the problem of reducing woody and herbaceous vegetation which competes with desired coniferous trees (McCormack 1985, Walstad and Kuch 1987, Lautenschlager 1990, Newton et al. 1992). Use of herbicides or manual methods as vegetation management tools are usually applied to early successional forest habitats for conifer release. This "release" from competing vegetation has consistently increased growth and survival of crop trees (Walstad and Kuch 1987), although herbicide treatments are consistently superior.

Herbicide related changes in wildlife habitat (food and cover) are a major environmental concern (Lautenschlager 1986, Freedman 1991). Recent studies (Newton et al. 1984, USDA 1984, Atkinson 1985, Feng and Thompson 1990) document that herbicides, properly used for conifer release, pose minimal toxicological hazard for terrestrial vertebrates. Several studies, reviewed by Lautenshlager (1993), have documented the response of small mammal populations to herbicide-induced habitat alteration in these young coniferous forests. In general, small mammal responses are species specific: some species are unaffected, while some select and others avoid herbicide-treated areas. Although much work has been conducted on the effects of herbicides on small mammals and their habitats, no studies followed small mammal populations and habitat changes for more than 4 years post-treatment (Sullivan 1990a, b). Indeed, valid generalizations about the effects of these treatments on small mammals are limited to one, or two, growing seasons after treatment (Lautenschlager 1993).

There is a paucity of long-term studies on herbicide use in the forest environment. This is particularly relevant to concerns regarding the potential long-term toxicological effects of herbicides on wildlife. Thus, this study was designed to test the hypothesis that (1) abundance and related demographic parameters of small mammal populations, and (2) species diversity of small mammal

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communities, would be adversely affected in herbicide-treated habitats at 9 and 11 years after treatment in coastal coniferous forest.

Materials and Methods

Description of Study Areas

This study was located at the University of British Columbia Malcolm Knapp Research Forest near Maple Ridge, B.C., Canada (49°16'N; 122°34'W) on sites in the Coastal Western Hemlock (CWH_{dm}) biogeoclimatic zone (Meidinger and Pojar 1991) between 140 and 400 m elevation. Paired control-treatment sites comprised the 9-year post-treatment (PT) study area. The control site (24.0 ha) was clear-cut harvested in 1973, slash-burned in the fall of 1974, and planted with Douglas-fir (*Pseudotsuga menziesii*) in the spring of 1975. The area was previously covered with a mature (70- to 90-year-old) forest dominated by western hemlock (*Tsuga heterophylla*), Douglas-fir and western red cedar (*Thuja plicata*) (Feller 1977). Cover included well decomposed slash with an abundance of deciduous trees, shrubs and herbaceous vegetation. Associated with the Douglas-fir stand were western hemlock natural regeneration and deciduous tree species such as red alder (*Alnus rubra*) and paper birch (*Betula papyrifera*). Shrub species included salal (*Gaultheria shallon*), willow (*Salix* spp.), vine maple (*Acer circinatum*), black raspberry (*Rubus leucodermis*) and salmonberry (*Rubus spectabilis*). Bracken fern (*Pteridium aquilinum*) and fireweed (*Epilobium angustifolium*) were the dominant herbaceous annual species. The treatment site (23.1 ha) was also clear-cut in 1973 and planted with Douglas-fir in 1975. This area was not burned. The previous forest was also dominated by mature western hemlock, mixed with Douglas-fir and western red cedar. The main cover was well decomposed slash with a similar vegetation composition as the treatment site. Control and treatment sites were separated by approximately 1.2 km which was a sufficient distance to limit small mammal dispersal between the two sites.

Paired control-treatment sites also comprised the 11-year PT study area. The control site was originally an untreated young successional stage reported by Sullivan and Sullivan (1981, 1982), but because of subsequent silvicultural treatments, this site had to be replaced for the current study. Therefore, a new control site (5.0 ha) clear-cut harvested and slashburned in 1958 and planted with Douglas-fir in 1959 was selected for sampling in 1990. This site was previously occupied by a forest composed of Douglas-fir, western hemlock, and western red cedar which originated after a wildfire in 1868. Because of comparable stand histories, we assumed that this site had a similar vegetative succession to that of the treatment. This site was dominated by Douglas-fir with a minor component of western hemlock, western red cedar, red alder, and cascara (*Rhamnus purshiana*) in the overstory. The understory was composed of salmonberry and sword fern (*Polystichum munitum*) with some salal, red huckleberry (*Vaccinium parvifolium*), thimbleberry (*Rubus parviflorus*), trailing blackberry (*Rubus ursinus*), deer fern (*Blechnum spicant*) and spiny woodfern (*Dryopteris assimilis*).

The treatment site (15.0 ha) was harvested and burned in 1959. A Douglas-fir plantation was established in 1960. This site was previously occupied by the same forest composition which originated from the 1868 wildfire. Dominant vegetation on this site in 1979 was Douglas-fir, vine maple, red alder, bitter cherry (*Prunus emarginata*), and bigleaf maple (*A. macrophyllum*), with an understory of salmonberry, sword fern, and elderberry (*Sambucus racemosa*). In 1990, this site had a similar species composition to that of the control. Control and treatment sites were separated by approximately 2.0 km.

Application of Herbicide

The 9-year treatment area (14.2 ha of the 23.1-ha site) was aerially sprayed with Roundup® (or Vision®) herbicide[1] at the rate of 3.0 kg/ha of active ingredient on 18 June 1982.

The 11-year treatment area (4.9 ha of the 15.0-ha site) was aerially sprayed with Roundup® at the rate of 2.2 kg/ha of active ingredient on 12 September 1979.

Small Mammal Populations

One sampling grid (1 ha) was located in each of the 2 control and 2 treatment sites. On each grid, 49 (7 x 7) trap stations were located at 14.3-m intervals and one Longworth live-trap was placed within a 2-m radius of each station. Traps were baited with peanut butter, whole oats, and coarse

[1]Commercial formulations (trademarks of Monsanto Company) containing glyphosate, 356 g/L present as isopropylamine salt

brown cotton was supplied as bedding. Traps were set on day 1, checked on days 2 and 3, and then locked open between trapping periods. The four grids were live-trapped at 3-week intervals from May to November 1990, which was 9 and 11 years after treatment, respectively, for the two study areas. For the 9-year PT study area, the sampling grids were originally live-trapped from April 1981 to September 1983 and from April to October 1985. For the 11-year PT study area, the sampling grids were live-trapped from July to November 1978, May to November 1979, and April to November 1980.

All small mammals (except shrews, *Sorex* spp., American shrew-moles, *Neurotrichus gibbsii,* and weasels *Mustela* spp.) captured were ear-tagged with serially numbered fingerling fish tags, sexed, reproductive condition noted, and weighed on Pesola spring balances. Reproductive performance was noted by palpation of male testes and mammaries of the females (Krebs et al. 1969). Small mammals were released on the grids immediately after processing. The major small mammal species captured included the deer mouse (*Peromyscus maniculatus*), and Oregon vole (*Microtus oregoni*). Other less common species sampled included the Townsend chipmunk (*Tamias townsendii*), southern red-backed vole (*Clethrionomys gapperi*), long-tailed vole (*M. longicaudus*), and Pacific jumping mouse (*Zapus trinotatus*).

Body weight was used as an index of age. For the numerically dominant deer mice and Oregon voles, animals were classified as juvenile or adult by weight (deer mice: juv = 0-16 g, adult ≥ 17 g; voles: juv = 0-20 g, adult ≥ 21 g) after Sullivan (1990b). Juveniles were considered to be young animals recruited during the study. Recruits were defined as new animals that entered the population through reproduction and immigration.

Demographic Analysis

Minimum number of animals known to be alive (MNA) (Krebs 1966) was calculated for populations of deer mice and Oregon voles. MNA was selected (Hilborn et al. 1976) because the generally preferred Jolly-Seber probabilistic estimator (Seber 1982) became unreliable and impossible to calculate for voles and chipmunks with low recaptures of previously marked animals (Krebs et al. 1986). Boonstra (1985) found that the MNA and Jolly-Seber techniques provided similar estimates of small mammal population size under field conditions when trappability exceeded 50%. The total number of individuals captured was used to compare control and treatment populations of southern red-backed voles, long-tailed voles, Pacific jumping mice, and American shrew-moles; and MNA was calculated for Townsend chipmunks.

Minimum survival rates for all males and females in control and treatment populations of deer mice and Oregon voles were summed over each summer period with an individual animal being tallied each time it was captured. Early juvenile survival, defined as the percentage of observed juveniles/expected number of juveniles, was calculated for deer mice and Oregon voles. Expected number of juveniles was the product of the number of successful pregnancies (based on consecutive captures of lactating females) and the average number of juveniles per litter as recorded in the literature: 4.5/litter for the deer mouse (Sheppe 1963, Sadleir 1974): 3.2/litter for the Oregon vole (Gashwiler 1972).

Mean body weights of male deer mice and Oregon voles during summer periods were used as an index of condition within control and treatment populations. Female weights were omitted because these data are complicated by undetected pregnancies, and hence tend to be more variable than those for males.

Species Richness and Diversity

Species richness was measured by the total number of species sampled (Krebs 1989). Species diversity was measured by Simpson's index of diversity (Simpson 1949) which is sensitive to changes in the more abundant species. The Shannon-Wiener index of diversity (Pielou 1966) was also used because it is sensitive to changes in the rare species in a community sample. These diversity measures were calculated using MNA values for the three common species and number of individuals captured for the less abundant species in a given sampling period and represented by an average value for each year.

Statistical Analysis

Average density of animals per ha and 95% confidence limits were calculated for the populations of deer mice and Oregon voles in all pre- and post-treatment periods for each study area. A paired

sample *t*-test was used to compare average density of shrew populations between control and treatment sites for the 9- and 11-year PT study areas. A chi-square analysis was used to compare proportion of breeding animals, observed versus expected number of juveniles, and total minimum survival rates for summer periods between paired control and treatment populations. Because some samples were not completely independent, these comparisons were used as an indication of the degree of difference between sets of data. Comparison of body weights and average diversity values between control and treatment populations was done with average values and 95% confidence limits. In all analyses, the level of significance was at least $P = 0.05$.

Results

Abundance

Average density of deer mice during summer periods from 1981 to 1990 indicated a lower abundance in the treatment than control in the immediate post-treatment period (1982), with comparable numbers in 1983, 1985, and 1990 (Fig. 1A). Average density of deer mice during summer sampling periods on 11-year sites was similar between control and pre-treatment sites in 1978, higher on the pre-treatment than control in 1979, and similar in the post-treatment years of 1980 and 1990 on control and treatment sites (Fig. 1B).

Average density of Oregon voles was similar between control and treatment sites in the 9-year PT study area up to 1990 (Fig. 2A). As in the 9-year area, the treatment population of voles was higher than the control at the 11-year area in 1990 (Fig. 2B). Average density of voles was higher on the control than treatment site in 1978 to 1980 at the 11-year area.

Average densities of shrews per trapping period provided a relative abundance of this insectivore on control and treatment areas, despite a high mortality because of the overnight trapping technique. Before treatment there were 2.1 times as many shrews per ha on the treatment than control site at the 9-year PT study area in 1981 (Table 1). There was, however, no statistical difference ($t = -1.46$, $P = 0.21$) in average density of shrews between control and treatment sites over the period of this study. At the 11-year PT study area, average densities of shrews were similar between control and treatment sites before treatment (1978, 1979) and during the first post-treatment year (1980). There were, however, 1.9 times as many shrews on the treatment than control site in 1990 (Table 1). Overall, there was no difference ($t = -1.32$, $P = 0.30$) in average density of shrews during the course of this study.

Details of changes in abundance of these two rodent species and *Sorex* spp. prior to 1990 are reported in Sullivan and Sullivan (1982) and Sullivan (1990a).

Reproduction

There were no differences in proportion of breeding males between control and treatment populations of deer mice at either of the 9- or 11-year PT study areas in 1990. There were significantly more reproductive female deer mice in the control than treatment population in 1990 for the 9-year PT, but no difference for the 11-year PT study area. There were no significant differences in proportion of breeding Oregon voles between control and treatment populations in 1990 at either study area.

The control population of deer mice had twice as many successful pregnancies as the treatment population in 1990 at the 9-year PT study area, with the same number (19) at the 11-year PT study area (Table 2). However, percentage recruitment of juvenile deer mice in control and treatment populations was similar at both areas. The number of successful pregnancies for Oregon voles tended to be higher in treatment than control populations. This was reflected in the significantly higher (3.2 times) percentage of recruits on treatment than control sites at the 9-year PT study area, and relatively higher (2.2 times) numbers treatment vs. control at the 11-year PT study area (Table 2). Details of this measure of reproductive success and early juvenile survival on these areas prior to 1990 are reported in Sullivan and Sullivan (1981) and Sullivan (1990b).

Survival

Total survival of deer mice and Oregon voles during summer periods showed no consistent differences between control and treatment populations in 1990 at the 9-year nor 11-year PT study areas.

Body Weight

Populations of male *P. maniculatus* had similar body weights during summer 1990 at the 9-year PT study

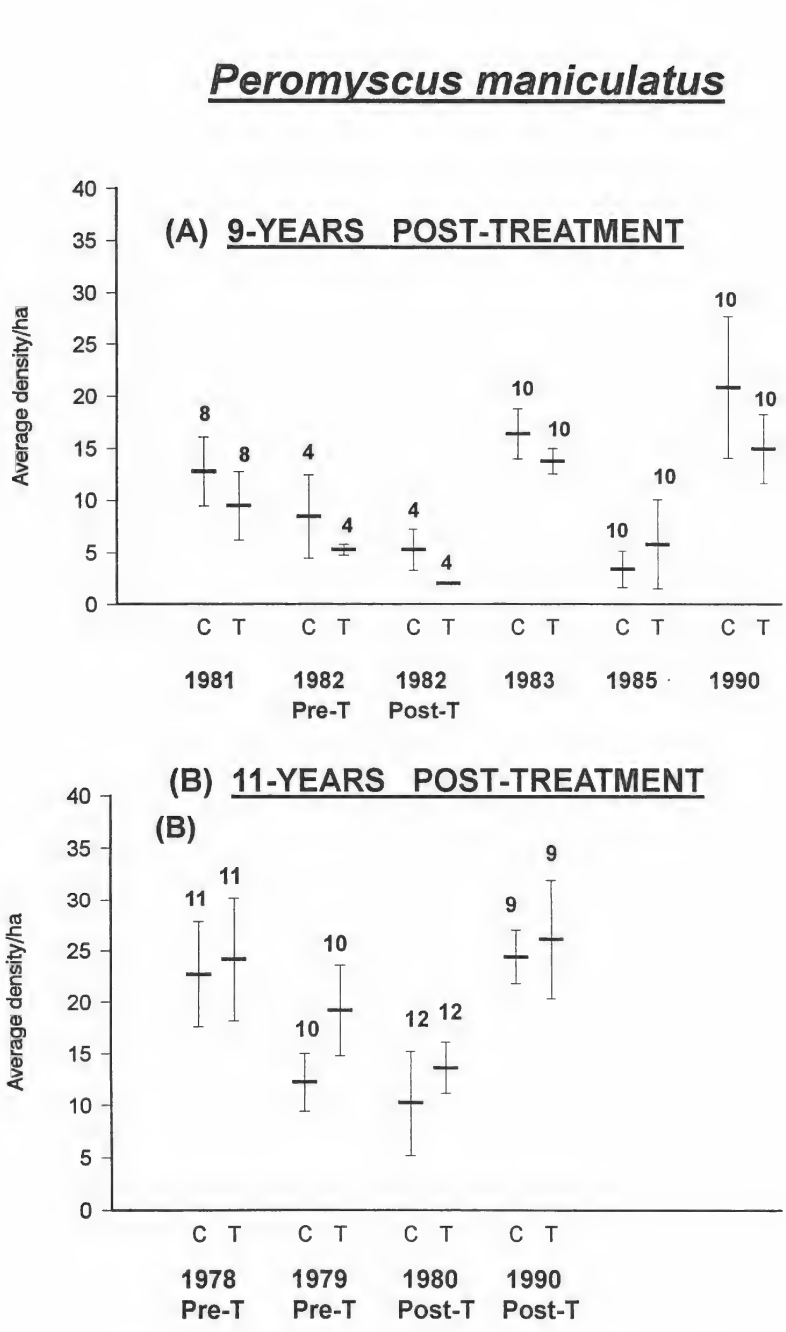

Figure 1. Average population density with 95% confidence limits of *Peromyscus maniculatus* on control and treatment sites at the (A) 9-year PT study area, and (B) the 11-year PT study area. Sample size (number of trapping periods) above upper limit. C = control; T = treatment.

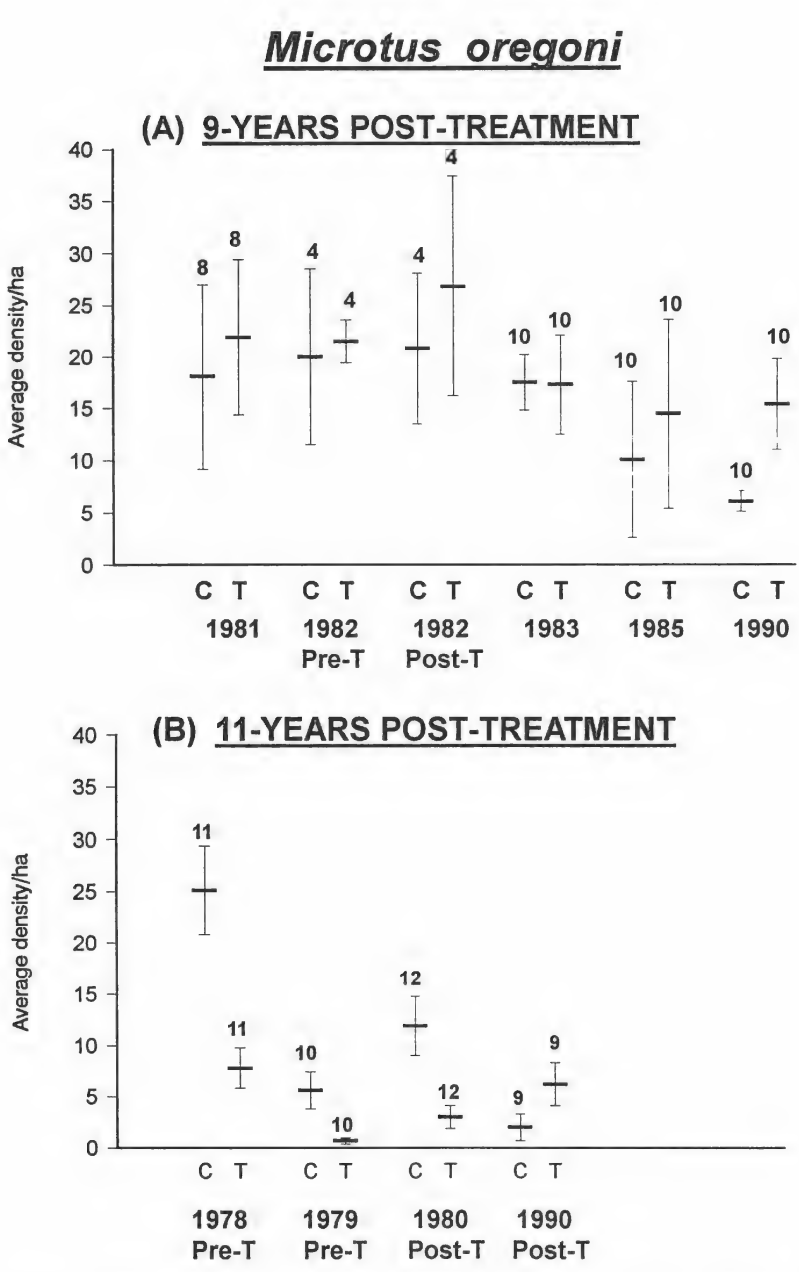

Figure 2. Average population density with 95% confidence limits of *Microtus oregoni* on control and treatment sites at the (A) 9-year PT study area, and (B) the 11-year PT study area. Sample size (number of trapping periods) above upper limit. C = control; T = treatment.

TABLE 1. Average density of individual shrews (*Sorex* spp.) captured per ha on control and treatment sites in the 9-year and 11-year post-treatment (PT) study areas.

Study area and year	Number of sampling periods	Control	Treatment
9-year PT			
1981 pre-T	8	2.6	5.5
1982 pre-T	4	3.0	2.5
1982 post-T	4	3.5	4.8
1983 post-T	10	1.3	1.9
1985 post-T	10	2.0	1.9
1990 post-T	10	1.5	1.7
11-year PT			
1978 pre-T	11	1.6	2.8
1979 pre-T	10	3.3	3.5
1980 post-T	12	3.1	2.6
1990 post-T	9	1.9	3.7

area with average values and 95% confidence limits in the control (15.8 g; 15.2-16.5) and treatment (16.2 g; 15.6-16.9), respectively. *M. oregoni* had heavier male animals in the control (22.6 g; 21.8-23.4) than the treatment (20.5 g; 19.6-21.5) in 1990. However, adult male voles tended to be heavier in the treatment (24.1 g; 23.5-24.7) than control (23.2 g; 22.8-23.5).

At the 11-year PT study area, populations of male deer mice in 1990 had similar average body weights in the control (15.6 g; 15.0-16.3) and treatment (15.0 g; 14.5-15.4), respectively. Populations of *M. oregoni* were also similar in average body weight in 1990 in the control (21.3 g; 17.1-25.6) and treatment (17.7 g; 15.5-19.8), respectively.

Species Richness and Diversity

Species richness of the small mammal communities was similar between control and treatment sites for all periods at the 9-year PT study area (Fig. 3A). Both measures of species diversity also followed this pattern with average values ranging from 0.47 to 0.67 for Simpson's Index (Fig. 3B) and from 1.34 to 1.74 for Shannon-Wiener (Fig. 3C). At the 11-year PT study area, species richness was similar between control and treatment sites but diversity declined in 1979 on the pre-treatment, and in 1980 on the post-treatment, compared with the control site (Fig. 4A). This decline coincided with the drop in Oregon vole abundance (Fig. 2B). Species diversity tended to be higher on the treatment than control in 1990 (Figs. 4B and C).

Discussion

Experimental Design

This study investigated the 9- and 11-year responses of small mammal populations to herbicide use for conifer release in young (7-year-old) and older (20-year-old) Douglas-fir plantations, respectively. Based on the classification of forest successional stages in western North America (Thomas et al. 1979), over the decade since treatment, the 7-year-old plantation changed successionally from the shrub-seedling stage to pole-sapling (16 years old) and the 20-year-old plantation changed from the pole-sapling to young (31 years old) stand stage.

TABLE 2. Successful pregnancies for *Peromyscus maniculatus* and *Microtus oregoni*, and observed and expected numbers of juveniles recruited into control and treatment populations during 1990 for the 9-year and 11-year post-treatment (PT) study areas. Percentage of juveniles (observed/expected) is given in parentheses.

	P. maniculatus		*M. oregoni*	
	Control	Treatment	Control	Treatment
9-year PT				
No. of successful pregnancies	12	6	7	10
Expected no. of juveniles	54.0	27.0	22.4	32.0
Observed no. of juveniles	40 (74.1)	26 (96.3)	10 (44.6)[a]	45 (140.6)[a]
11-year PT				
No. of successful pregnancies	19	19	4	7
Expected no. of juveniles	85.5	85.5	12.8	22.4
Observed no. of juveniles	39 (45.6)	44 (51.5)	5 (39.1)	19 (84.8)

a-a, $P < 0.01$. Values followed by same letter are significantly different by Chi-square.

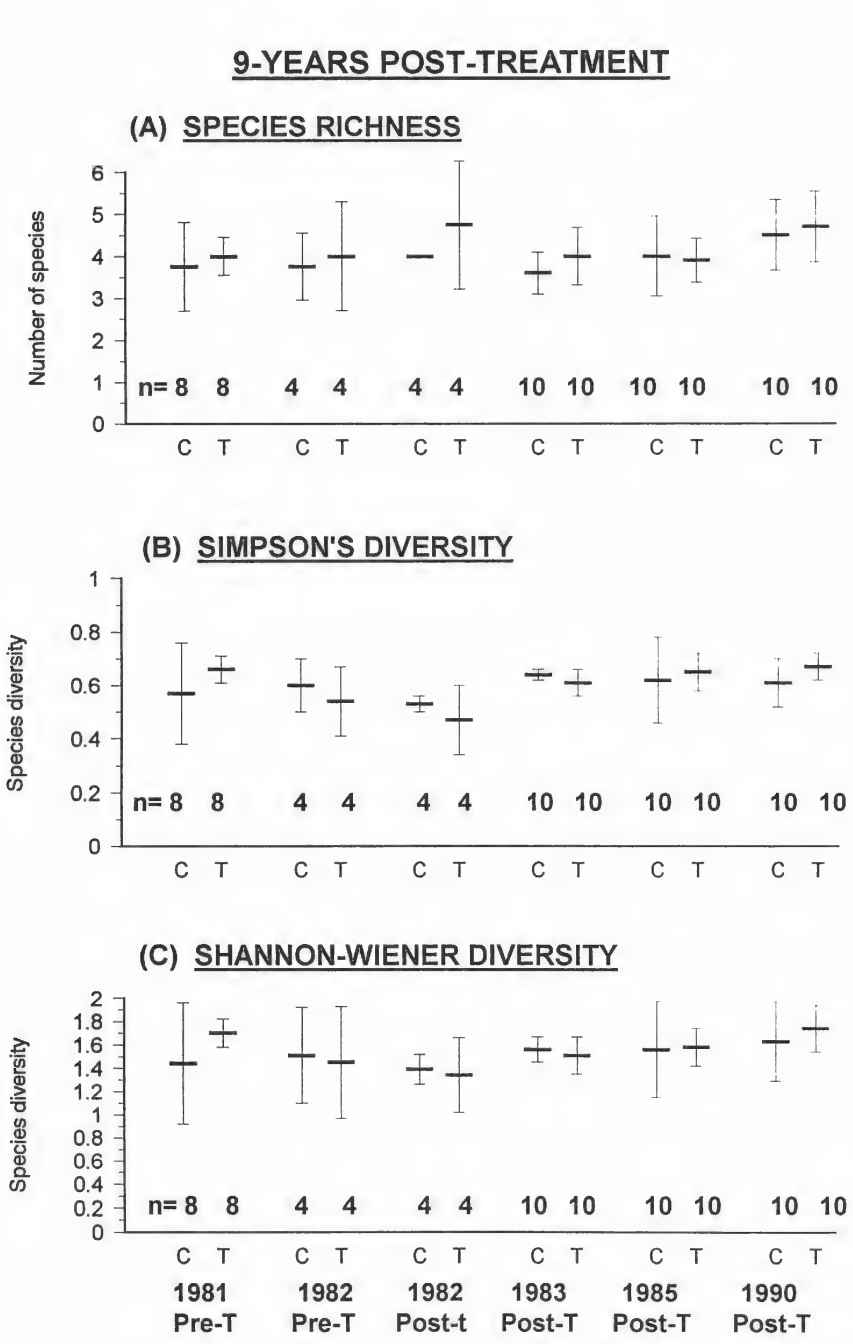
9-YEARS POST-TREATMENT
(A) SPECIES RICHNESS
Number of species
n= 8 8 4 4 4 4 10 10 10 10 10 10
C T C T C T C T C T C T
(B) SIMPSON'S DIVERSITY
Species diversity
n= 8 8 4 4 4 4 10 10 10 10 10 10
C T C T C T C T C T C T
(C) SHANNON-WIENER DIVERSITY
Species diversity
n= 8 8 4 4 4 4 10 10 10 10 10 10
C T C T C T C T C T C T
1981 Pre-T
1982 Pre-T
1982 Post-t
1983 Post-T
1985 Post-T
1990 Post-T

Figure 3. Species richness (A), Simpson's diversity (B), and Shannon-Wiener diversity (C) for small mammal communities on control and treatment sites at the 9-year PT study area. C = control; T = treatment. n = number of trapping periods.

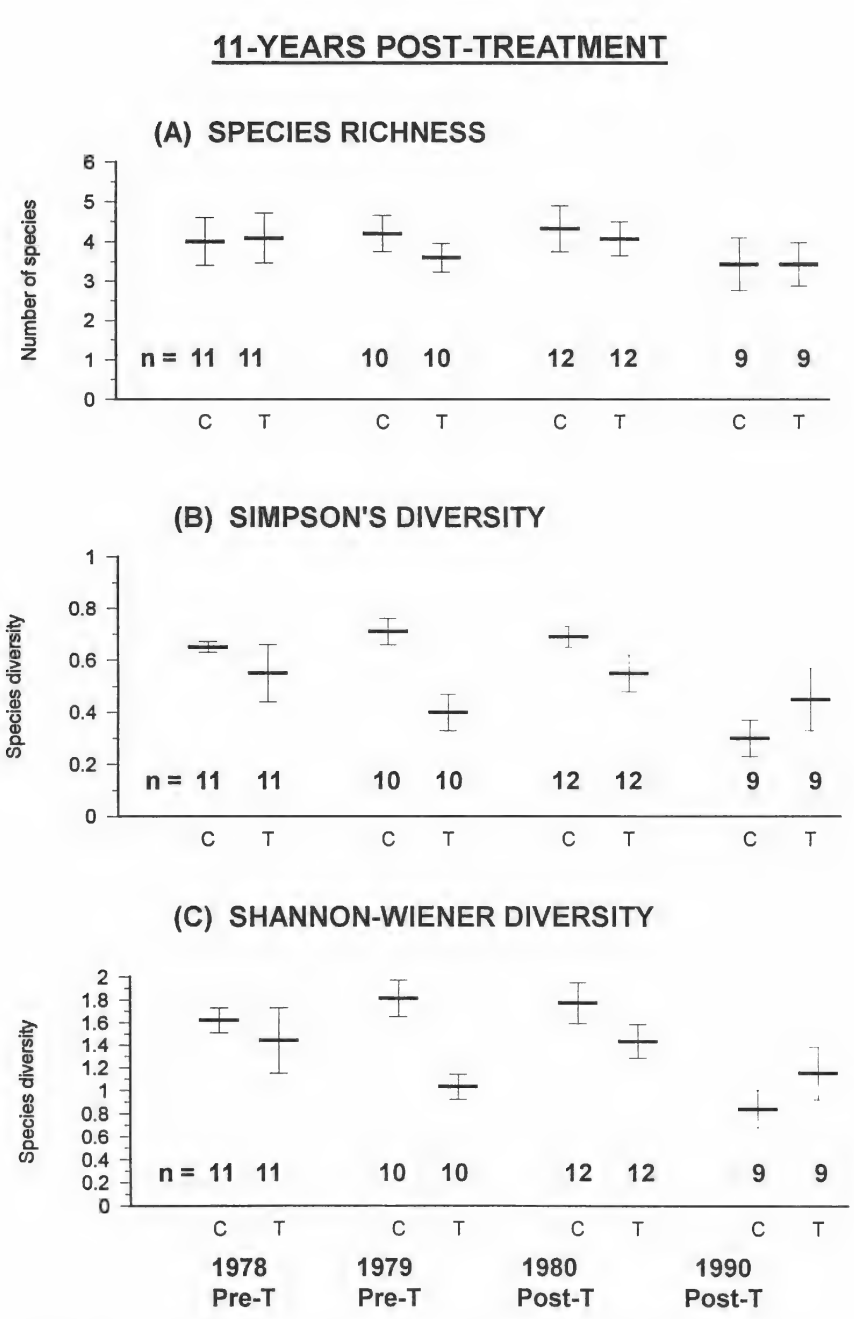

Figure 4. Species richness (A), Simpson's diversity (B), and Shannon-Wiener diversity (C) for small mammal communities on control and treatment sites at the 11-year PT study area. C = control; T = treatment. n = number of trapping periods.

This difference in successional stage precludes the classification of these control-treatment pairs as true replicates (Hurlbert 1984) and our results should be interpreted accordingly. Although we did not have similarity of sites and timing of treatments for adequate replication, pre-treatment sampling was conducted at both study areas and long-term response data were collected. Thus, two of the three requirements were met for providing accuracy and predictive power in forestry-wildlife studies (Lautenschlager 1993).

The 9-year PT study continued on the same control and treatment sites (1981 to 1985) initially reported by Sullivan (1990a, b) using exactly the same grid positions and methods of intensive sampling of the small mammal communities. In the 11-year PT study, the control site (1978 to 1980) had to be changed from that reported by Sullivan and Sullivan (1981, 1982) to a 30-year-old Douglas-fir stand with a similar history to that of the treatment. Identical sampling methodology (and grid position for the treatment) was also used for this study area. Again, however, our results must be viewed within the context of this confounding factor of a "new" control.

Another difference between our two study areas was the June and September applications of herbicide. The June application provided pre-treatment and post-treatment periods within the summer of 1982 since there was clearly a dramatic change in habitat during the growing season (Sullivan 1990a). The mid-September application was at the end of the growing season and herbicide-induced leaf-fall could not be distinguished from that occurring naturally (Sullivan and Sullivan 1982). Thus, both summers of 1978 and 1979 were considered pre-treatment years for the 11-year PT study.

Successional Stage and Herbicide Treatment

Although not documented by data on habitat structure, our control and treatment areas changed dramatically as vegetative succession occurred over the post-treatment decade. Most herbicide-induced changes in herbaceous vegetation persist for only 2-3 years, whereas impacts on shrub species may be considerably longer (Lautenschlager 1990, Newton et al. 1992, Freedman et al. 1993, Sullivan et al. 1996a). Habitat alteration from these herbicide treatments appeared to have little effect on the distribution and abundance of small mammal populations in the immediate post-treatment years (Figs. 1 and 2; Sullivan and Sullivan 1982, Sullivan 1990a). Other studies in the Pacific Northwest have reported that the application of several herbicides altered the species composition of small mammal communities in Oregon one year after treatment (Black and Hooven 1974, 1979). Similar results were obtained for glyphosate herbicide in the first year after treatment with a return to prespray conditions in the second year (Anthony and Morrison 1985). Cole et al. (1996) reported little change in small mammal populations after herbicide treatment in hardwood conversion areas. Similarly, Runciman and Sullivan (1996) found no significant effects of manual cutting or cut-stump herbicide treatment on small mammal populations two years post-treatment.

It is likely that post-harvest successional change in vegetation has more of an impact on small mammals than that induced by a herbicide treatment. Abundance of deer mice was generally similar on control and treatment areas over the post-treatment decade in the transition from shrub-seedling to pole-sapling to young stand stages. This is not surprising as *P. maniculatus* occupies many different habitats ranging from open fields to old growth forests (Baker 1968).

The higher abundance of Oregon voles on the treatment than control at 9-11 years after herbicide application suggests that openings in the plantations encouraged development of understorey herb and shrub species that persisted through time. In 1990, *M. oregoni* populations were, on average, 2.5-3.1 times higher in the pole-sapling (9-year PT) than young (11-year PT) stand. This difference in vole numbers was also evident between control (shrub-seedling) and treatment (pole-sapling) sites in 1978-1980 (Fig. 4B, Sullivan and Sullivan 1982). The Oregon vole occurs primarily in early successional stages after logging as well as in the edges of timber and abandoned brushland (Gashwiler 1970, 1972, Hooven and Black 1976, Sullivan 1980, Sullivan and Krebs 1981). Because canopy closure in our 30-year-old plantations averaged 90% (P. Sanders, pers. comm.), it is not surprising that Oregon vole numbers were low. In addition, Townsend's chipmunks were essentially absent from these stands, since they prefer high quality habitat associated with early successional stages after harvesting (Tevis 1956, Anthony and Morrison 1985), mature-old growth forests (Gashwiler 1959, Rosenberg and Anthony 1993), and riparian areas in second-growth coniferous forests (Anthony et

al. 1987). Where the canopy is opened by stand thinning or conifer release treatments, understory development can provide habitat for various early successional species.

Demography and Diversity

As discussed by Newton et al. (1984), it is likely that small mammals do have some glyphosate residues within their body systems during the post-treatment period. What, then, are the potential long-term (10-year) effects of these residues on demographic attributes of small mammals such as the deer mouse and Oregon vole? Our results suggest that this forest herbicide did not adversely affect reproduction, survival, or growth of animals in treatment areas a decade after application. These results are consistent with earlier studies 4 years post-treatment in coastal coniferous forest (Sullivan 1990b) and 5-years post-treatment in sub-boreal spruce forest (Sullivan et al., unpubl. manuscript).

Species richness and diversity of the small mammal communities showed little change over the decade since treatment. The lower diversity indices on the pre-treatment in 1979 and post-treatment in 1980 can be linked to low vole numbers. Similarly, the lower species diversity on the control than treatment areas in 1990 is likely due to lower numbers of voles and the absence of chipmunks. This lack of change in diversity is similar to the result reported for small mammal communities in sub-boreal spruce forest (Sullivan et al., unpubl. manuscript).

Thus, this study provides the first truly long-term investigation of the effects of forest herbicide use on demography and diversity of small mammal communities. Despite the lack of suitable replicates, we reject the hypothesis that these attributes would be adversely affected in herbicide-treated habitats at 9 and 11 years after treatment.

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A Supercolony of the Thatch Ant *Formica obscuripes* Forel (Hymenoptera: Formicidae) from the Blue Mountains of Oregon

Abstract

Foliage-foraging ants have often been demonstrated to be important predators of tree defoliating insects such as western spruce budworm. Because of the importance of ants as pest suppression agents, we were interested in describing a rare supercolony of western thatching ants (*Formica obscuripes* Forel) from the Blue Mountains of northeastern Oregon. The supercolony occupies a site within a second-growth mixed-conifer stand near Lehman Hot Springs, approximately 20 km east of Ukiah, Umatilla County, Oregon. In October 1993, the 4-hectare colony had 210 active nests, with the largest nest having an aboveground volume of 6 m^3. Location of primary nests was not related to canopy cover, although nests tended to be associated with stumps and down woody debris. Nest excavations in May and June 1995 allowed estimation of the total nestbound population for the supercolony at 56 million individuals; addition of the foraging population would increase this estimate substantially. We estimate that to maintain the current worker population the supercolony would require at least 470 kg dry weight of food from its foraging territory annually, or about 11 times the total dry weight of western spruce budworm that might typically occupy the site at any given time during an outbreak. Thatching ants may have had a significant effect on populations of defoliating insects at Lehman Hot Springs during the last western spruce budworm outbreak (1980-1992), since the forest stand occupied by the supercolony was visibly less defoliated than the surrounding mixed-conifer stands.

Introduction

Species of the *Formica rufa*-group (thatching ants of North America and red wood ants of northern Europe and Asia) have received considerable attention as predators of forest pests. Thatching ants are ecologically dominant ants that tend Homoptera for honeydew, as well as scavenge and prey on a wide variety of terrestrial arthropods (Weber 1935, Cherix and Bourne 1980, Skinner 1980, MacKay and MacKay 1984). In mixed conifer forests of Europe, *rufa*-group species have historically been encouraged for their beneficial effects in controlling populations of forest insect pests (Otto 1962, McNeil et al. 1978). Their beneficial influence is documented in North America as well, as predators of western spruce budworm (*Choristoneura occidentalis* Freeman)(Youngs and Campbell 1984, Torgersen et al. 1990), and gypsy moth (*Lymantria dispar* (L.))(Smith and Lautenschlager 1981).

In North America, Europe, and northern Asia, colonies of at least 13 *Formica rufa*-group species have been reported to exhibit "polydomy," in which the colony is composed of more than one primary nest (Marikovsky 1962, Talbot 1971, Imamura 1975, Higashi and Yamauchi 1979, Mabelis 1979, Rosengren 1979, Cherix and Bourne 1980, Kloft et al. 1973, MacKay and MacKay 1983, Wheeler and Wheeler 1986, Rosengren et al. 1985, O'Neill 1988). In general, small colonies composed of fewer than about 100 nests are termed "supranests," while larger colonies occupying hundreds of nests are termed "supercolonies" (Rosengren et al. 1985).

This paper describes a supercolony of 210 nests of the western thatching ant *Formica obscuripes* Forel in the Blue Mountains of northeastern Oregon. We addressed four objectives intended to identify the function of thatching ants in the forest ecosystem and the potential factors affecting their local distribution and abundance: 1) confirm colonial status, 2) describe the abundance and distribution of nests, 3) estimate total population size during the study period, and 4) determine the relation between forest structure and the distribution and abundance of nests. We also sought to determine whether other such populations of nests might exist in similar mixed-conifer stands elsewhere in the local geographical area.

Study Area and Species

The 4-ha study site is near Lehman Hot Springs (T5S, R33E, Sec. 12), about 20 km east of Ukiah, Umatilla County, Oregon. The mixed-conifer stand

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within which the site lies was dominated by grand fir (*Abies grandis* (Dougl. ex D.Don) Lindl) with a heavy component of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). The plant association at the site was grand fir/twinflower (CWF3 21 ABGR/LIBO-BLUE of Johnson and Clausnitzer 1992, pers. comm. F. C. Hall, USFS Plant Ecology Program). The site is on private land owned by the Lehman Hot Springs Development Corporation, which operates the hot springs as a recreational facility. The assemblage of nests was bounded on the north by a small abandoned sawmill in a clearing. Immediately to the east was the commercial recreation site associated with the hot springs. To the south and west were intensively managed stands of mixed conifers interrupted by a few logging roads. Many of the nearby stands were recently logged to harvest trees killed during an outbreak of western spruce budworm that ended in 1992.

Materials and Methods

Supercolony status was assessed in May 1995 by transferring workers among primary nests, and by observation of active trunk trails. For each transfer, a worker from the surface of the source nest was herded into a clean vial without direct handling and was held for at least 5 minutes before introduction to a different primary nest. We performed three sets of transfers of workers: 1) among nests within the 210-nest supercolony, 2) from an adjacent population of nests 300 m north to nests within the study population, and 3) from a Grande Ronde Valley colony of *Formica obscuripes* 50 km east of Lehman Hot Springs to nests within the study population. We assumed supercolony status if the following results were obtained: 1) transfers among nests within the Lehman supercolony did not result in worker rejection, 2) transfers from other populations resulted in rejection, and 3) primary nests within the supercolony were linked by a common trunk trail system.

To describe nest distribution, we laid out a 200-X 200-m (4 ha) study area, on 23 September and 7 October, 1993. Area boundaries were laid out to encompass the apparent extent of the supercolony. Study area boundaries were laid out with hand compass and marked with wire flags at 20-m intervals. We used compass and string lines to lay out intermediate grid-lines to form 100 20- X 20-m plots. Corners of plots were marked with wire flags. The location of nests within each plot was sketch-mapped. For each nest we recorded height, longest and shortest diameters, activity status (active—vigorous nest surface activity; declining—nest surface with few workers present; dead—no activity on nest surface), and classified the kind of wood, if any, with which the nest was associated (live tree, dead tree, stump, down wood). To examine the relation between forest structure and the distribution and abundance of nests, tree-crown closure was measured with a spherical densiometer at the center of each plot (Lemmon 1956). Four measurements of crown closure were made, each facing toward a side of the plot, and the mean of the four measurements was used to characterize crown closure within each plot. Regressions were calculated for crown closure means against both nest volume and number of nests per plot. The spatial pattern of ant nests was analyzed with nearest neighbor analysis, with the use of the refined nearest neighbor program (Moeur 1993, 1995).

To approximate nest shape for determining aboveground volume of nests, we measured height and long and short diameters. We assumed that nests were symmetric, with an elliptic base and parabolic profiles along the perpendicular planes running parallel to the major (x-y) and minor (y-z) axes of the ellipse (Figure 1). Other shapes were considered, but the elliptic-paraboloid model yielded nest shapes that were most visually faithful to the general shape of the nest.

We derived the equation for volume (V) as a function of nest height (h), 1/2 long diameter (l), and 1/2 short diameter (s):

$$V(h,l,s) = \frac{4}{3} hs \int_{-l}^{l} \left[1 - \left(\frac{x}{l}\right)^2\right]^{\frac{3}{2}} dx$$

To calculate nest volumes, we integrated this equation to yield:

$$V(h,l,s) = \pi \times \frac{h \times l \times s}{2}$$

To correlate nest volume and worker population we excavated six primary nests in May and June 1995. Nest material occupied by ants was

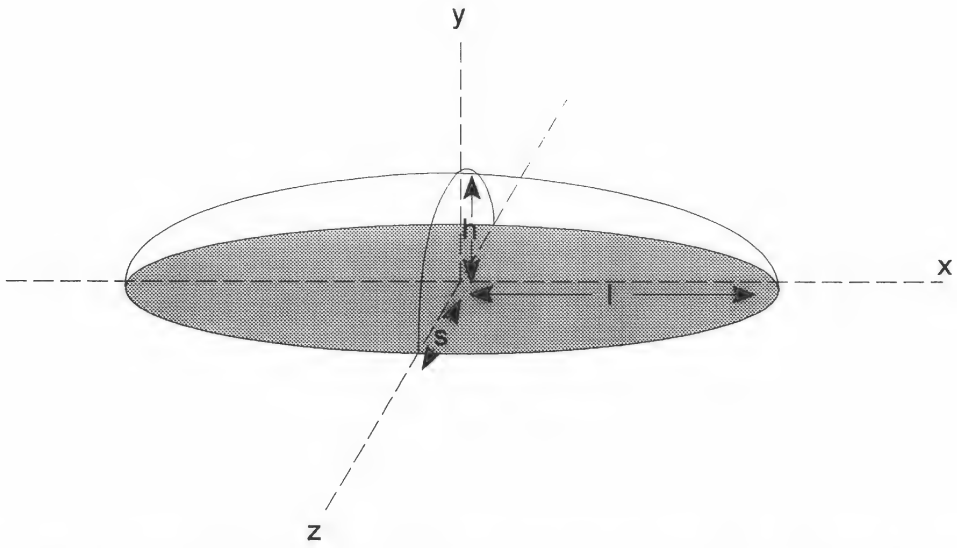

Figure 1. The elliptical-paraboloid shape used to compute aboveground volumes of ant mounds. V, volume; h, height; l, 1/2 long diameter; s, 1/2 short diameter; x, y, z axes.

pitchforked and shoveled into large PVC-coated nylon "dry bags"[1,2], mixed thoroughly, and weighed. Aboveground and belowground nest material was placed in separate bags. Three approximately 1-liter sub-samples each from aboveground and belowground nest material were then removed and weighed. In the laboratory, eggs, larvae, pupae, workers, and reproductives were sorted from the subsamples and counted. Mean counts from subsamples were then multiplied by the quotient of total nest weight and total subsample weight to obtain nestbound population sizes. A regression was calculated for aboveground volumes versus nest populations, and the resulting equation was used to estimate the population of each of the 210 active nests, the summation of which provided an estimate of population for the entire supercolony.

Assuming that nestbound population size was correlated with forager activity, the relation between mound volume and nestbound population size could be used to create an approximate visual image of forager activity at the site. Population sizes of active mounds were used as a third (vertical) dimension along with the x-y coordinates of nest locations to create the visual display. Population sizes were graphed with SigmaPlot for Windows (Jandel Scientific, 1994)[2]. The first step was to create a mesh-surface fit to the population at a high enough resolution to obtain a relatively smooth surface, with peaks and troughs reflecting areas of high and low forager activity. A contour graphing option was then selected on the mesh points of location versus forager activity. A log scale was used on the forager activity axis (reflecting the 3-dimensional nature of this quantity) and different line-densities were chosen for the major and minor contour intervals. The resulting image gives an approximation of nest distribution and forager activity at the site.

To determine whether supercolonies such as the Lehman colony might occur elsewhere in Blue Mountains mixed-conifer forests, we conducted a census on 161 km of transects. We selected varied locations for the transects within the Umatilla National Forest so that they would be representative of a range of habitats. Twelve transects (10 meters X 4 to 22 km) were examined between 7 and 21 October, 1993. Transects were laid out along the U.S. Forest Service road system within

[1]76.2 X 152.4 cm; "guitar bag"; 18 oz. nylon. Available from Cascade Outfitters, Springfield, Oregon, 97477.

[2]Mention of product or source is given for information only. It does not constitute endorsement of either by the U.S. Government.

Townships 4-6 S., and Ranges 29 and 30 E., about 20 km west of Ukiah, and 30 km northwest of the study colony. The area traversed was associated with the roads from Happy Home Spring to Thompson Flat Well on the west side of the area, and from Gulliford Spring to Divide Well on the east. A single examiner then walked along the transect, which was simply a walking-course that maintained a minimum distance of 200 meters from any road, and the area within 5 meters on each side of the transect was scanned for thatching ant nests.

Results

The total of 12 transfers among nests within the Lehman population typically resulted in resident worker acceptance of the introduced workers. In general, introduced workers were either ignored for parts of the 5-minute observation period, experienced occasional antennation from resident workers, and/or entered a nest entrance hole and disappeared. Of the four introduced individuals observed for the full 5-minute period, two experienced mild "mobbing" behavior by resident workers, in which several resident workers showed considerable interest but no aggressive behavior toward the introduced worker. To compare within-nest to among-nest behavior, we removed a number of nest-surface workers, held them for 5 minutes, and reintroduced them into their own primary nests. We observed no difference in the response of resident nest surface workers to resident re-introduced workers, compared to the response of residents to workers from other nests within the Lehman population—within-nest introductions also resulted in mild "mobbing" behavior, as well as occasional antennation and trophyllaxis.

By contrast, nest surface workers of the same species introduced from the Grande Ronde Valley population 50 km away were immediately attacked by resident workers, with each introduced worker attracting a locus of several residents. Attack consisted of pinioning and biting of introduced workers by resident workers, with introduced workers responding by biting and spraying from the poison gland. An intermediate response by resident workers was observed when nest-surface workers were introduced from the adjacent population 300 m north of Lehman Hot Springs. Upon transfer, introduced workers were immediately pinioned by resident workers for each of the seven 5-minute observation periods. Pinioning was not however, accompanied by additional aggressive behavior either on the part of residents or introduced workers. In summary, transfer experiments supported the hypothesis that the Lehman population was a "supercolony," and not a population of independent nests. The graded responses of resident workers to introduced workers from colonies 300 m and 50 km distant suggests that the adjacent population may be closely related to the Lehman population, perhaps owing to past nest fission events.

We also observed a complex network of trunk trails among nests within the Lehman population, with foragers moving freely along trails among nests. Transport of larvae, pupae, and adults along trunk trails was also observed, usually in one direction at any given moment of time. Hence, both transfer experiments and trunk trail observations strongly support the hypothesis that the Lehman population is a supercolony.

A total of 293 nests were recorded during the nest census, of which 210 were occupied by workers (Figure 2). Of the 210 occupied nests, 8 had aboveground volumes greater than 1000 liters, 92 ranged between 100 and 999 liters, 96 between 10 and 99 liters, and 14 were less than 9 liters in aboveground volume. The largest nests occurred in an arc from the southwest corner northward and then east toward the northeast corner. Fifty-one of the 100 20-meter plots contained fewer than two nests, while only eight contained more than six nests, giving the nests a left-skewed distribution at the 20 x 20 meter plot scale. Nearest neighbor analysis revealed clumping of nests at the scale of 3 to 12 meters (Figure 3). Observed nest distribution merged with the theoretical random distribution at scales of less than 3 meters and greater than 12 meters. Among active nests there was no relation between canopy cover and nest volume. Of the 210 active nests, 99 (47%) were associated with large down logs or slash (logs< 3 cm in diameter); these nests were also the largest in volume (312.0 liters $\pm$ 79.5 S.E.). There were 49 active nests (23%) located on stumps or against the bases of living trees, having only about half the volume (158.0 liters $\pm$ 34.0 S.E.) of the largest nests. The third group of 62 nests (29%) were not associated with any woody structure and were intermediate in aboveground volume (187.0 liters $\pm$ 26.0 S.E.).

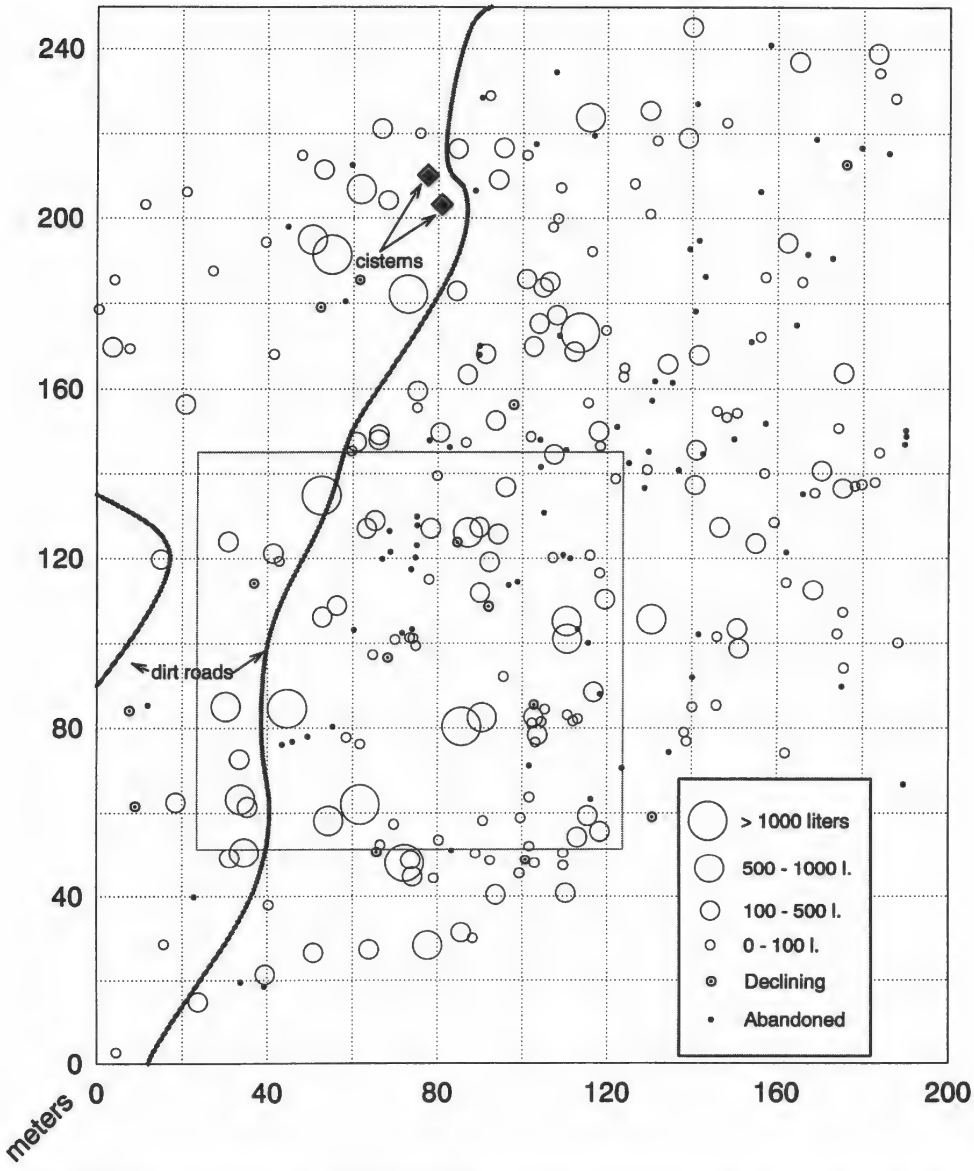

Figure 2. Distribution, aboveground nest volume size classes (in liters) and health status of ant nests at Lehman Hot Springs, Oregon, 1993. Symbols denote ranges of aboveground volume (liters) of nests calculated by Equation 2. Inset indicates area of supercolony shown in Figure 5.

A total of six primary nests were excavated in May and June 1995. We counted between 0.9% and 3.5% of the total individuals within each nest. The aboveground volumes ranged from 13.8 to 239.9 liters (Table 1). Proportions of the four developmental stages of ants varied considerably among excavated nests, with only two nests having an abundance of all stages. In general, we

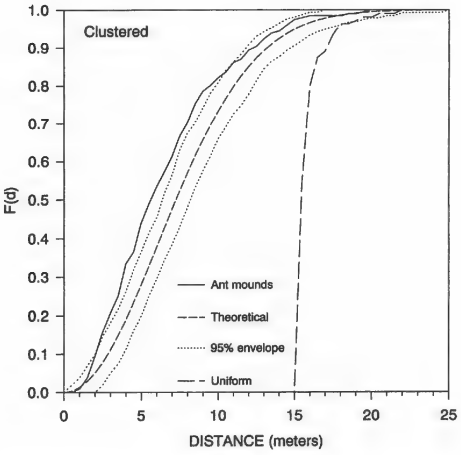

Figure 3. Cumulative nearest neighbor distribution for the 210 active thatching ant nests at Lehman Hot Springs, with $F_{(d)}$ = the proportion of nests having a nearest neighbor within distance d. Theoretical random distribution is given with a 95% confidence envelope, and a uniform distribution is provided for comparative purposes.

found more brood in the latter three excavations. Reproductives were found in four of the six nests; many of the queens had evident wing stumps, indicating that these had recently mated and been accepted into the nests. There was a significant correlation ($y = 0.944x + 42.93$; $r^2 = 0.56$) between aboveground nest volume and the estimate of total nestbound population (Figure 4). The nest excavated first had a significantly greater nestbound population than the nest of equivalent size excavated three weeks later. Without this early outlier, the r^2 for the latter set of five excavated nests was 0.93, rather than 0.56. The most conspicuous difference between the first excavation and the latter five was the weather—through most of April and early May conditions were cool and wet, but they changed to warm and dry by mid-May. During the latter half of May, the amount of worker activity on the surface of most nests declined substantially, probably because many workers were moving out into their foraging territories. Hence the early May excavation may have contained a large number of nestbound workers that had not yet left the nest for foraging duties.

When the correlation equation is applied to all 210 active nests, the estimate for the total nestbound population of the supercolony is 56,400,000 individuals, including sexuals and all developmental stages. Because foraging populations were not estimated, this figure can be considered a conservative estimate of supercolony population. Of the 210 active nests, 76 had estimated populations of between 10,000 and 99,000 individuals, 127 had between 100,000 and 999,000, and 7 nests were estimated to contain more than one million thatching ants. The largest nest had a volume of more than 6 m^3 and an estimated population of 6.1 million individuals.

After nest volumes were converted to nestbound ant numbers, a contour map was generated that depicts ant density within the supercolony (Figure 5). Assuming that the number of nestbound individuals reflects potential foraging activity, the contour map depicts the predicted spatial ecological effect of the supercolony.

The 161 km of nest-detection transects traversed diverse stand types and habitats: mixed-conifers, ponderosa pine, lodgepole pine, variants of these stands, riparian corridors and uplands, grassy scabflats, and edges. No thatching ant nests were found in the census.

TABLE 1. Aboveground nest size (liters), percent of total nest population counted (%Count), and estimates of eggs, larvae, pupae, workers, and queens for six nests excavated at Lehman Hot Springs study site, 9 May through 9 June 1995.

Nest	Date	Size (liters)	%Count	Eggs	Larv	Pup	Wrkrs	Queens	Total
1	9 May 95	66.5	1.75	0	0	0	236,000	500	236,500
2	22 May 95	65.4	2.09	0	190	0	36,900	0	37,090
3	22 May 95	13.8	3.50	0	0	0	17,400	100	17,500
4	31 May 95	239.9	0.90	7,980	10,800	3,430	223,000	1,020	246,230
5	9 June 95	148.2	1.94	1,040	17,800	10,200	169,000	180	198,220
6	9 June 95	38.5	3.33	1,790	340	0	59,200	0	61,300

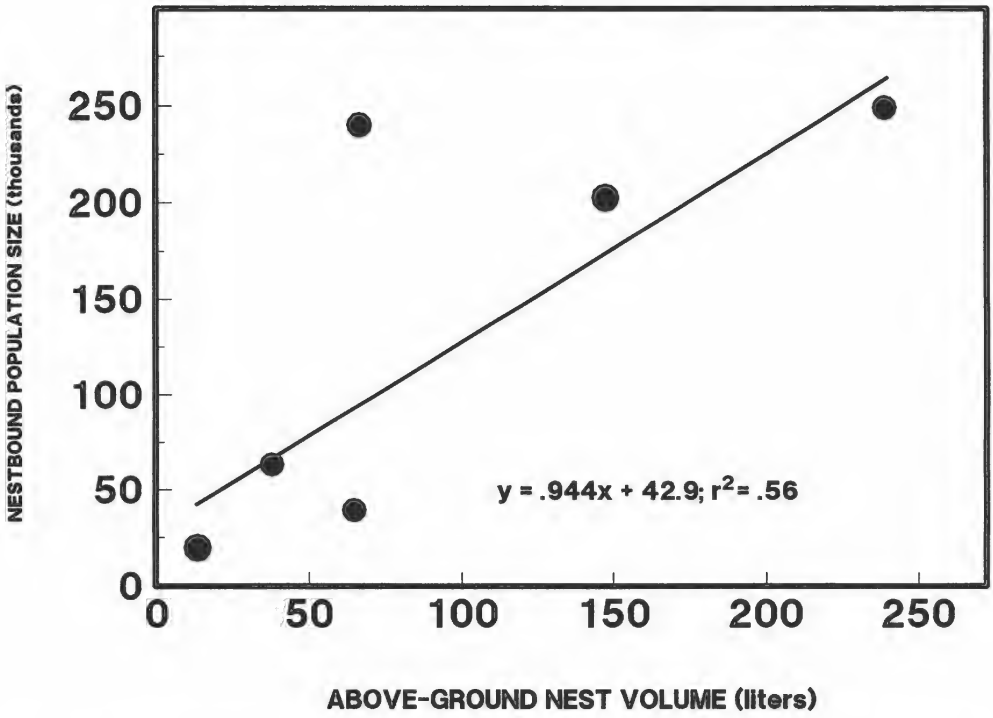

Figure 4. Correlation between aboveground nest volume and the number of nestbound individuals (data from nest excavations).

Discussion

Supercoloniality appears to be a plastic feature of most *Formica rufa*-group species. Both single nest colonies and supercolonies have been observed in at least 13 *F. rufa*-group species worldwide, including all of the species most intensively studied. Supercolonies range in size from a few nests (MacKay and MacKay 1983), to dozens of nests (Rosengren et al. 1985), to colonies composed of hundreds or even thousands of nests (Higashi and Yamauchi 1979). Supercolonies can occupy relatively small areas with a few large nests. For example, in Russia, Marikovsky (1962) found 111 nests with 140 million *F. rufa* individuals on 0.61 ha. In contrast, supercolonies can occupy more sparsely very large areas as described by Higashi and Yamauchi (1979), who tallied 45,000 nests with 306 million *F. yessensis* individuals on 2.7 km^2 in Japan. Presumably, differences in worker density are related to habitat type; the *F. rufa* supercolony described above was found in a forested habitat, while the *F. yessensis* supercolony occurred in a grassland. In support of this observation, the forest-dwelling supercolony described herein is much more similar in worker numbers, nest numbers, and area occupied to the forest-dwelling *F. rufa* colony described by Marikovsky.

Because supercolonies are composed of nests among which workers cooperate, the spatial arrangement of nests will be expected to differ from the situation in which individual nests compete. Indeed, the aggregated nest distribution within the Lehman supercolony may represent a history of reproduction by nest fission, and subsequent cooperation among nests, with the scale of aggregation (3-12 meters) reflecting the distance daughter colonies migrate from their parents. This among-nest aggregation contrasts sharply with the "over-dispersed" distributions observed in nearly all studies of ant populations composed of competing nests (Levings and Traniello 1981). Hence, overdispersion is the rule when among-nest

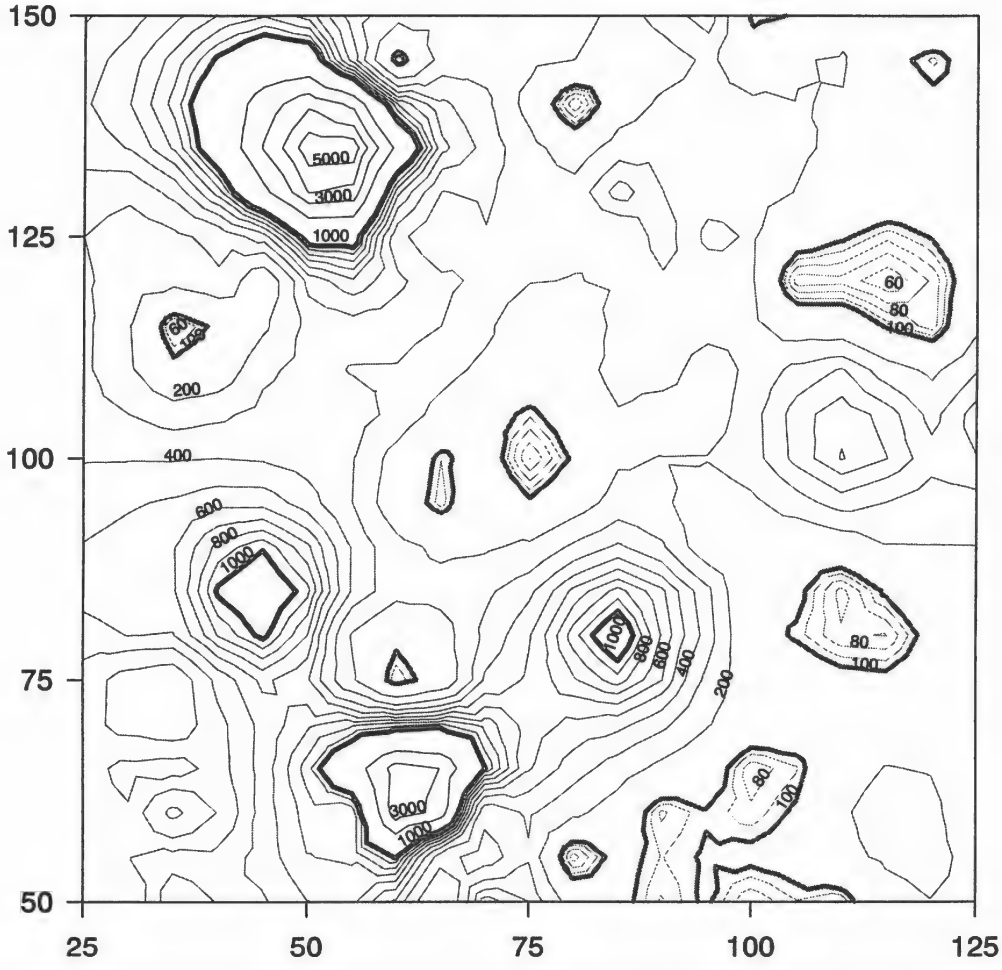

Figure 5. Contour map illustrating worker activity derived from correlation of nest volume and nest population size for the 100-X 100-meter area dilineated in Figure 2. Contours equal ants X 1,000.

territoriality occurs, while among-nest aggregation may be a general feature of supercoloniality.

Supercoloniality may increase colony fitness under certain conditions. Because supercoloniality results in decentralized foraging, energetic and microclimatic constraints imposed by a fixed central place are relaxed, allowing foraging range expansion (Rosengren and Pamilo 1983, Puntilla et al. 1994), increased domination of resources (Higashi and Yamauchi 1979, Cherix and Bourne 1980), and more economic defense of territory (Hölldobler and Lumsden 1980). Links among widely dispersed nests may also facilitate communication about food, disturbance, and potential new nest sites (Scherba 1964).

Several authors have observed differences in seasonal use of nests within supercolonies of *F. rufa*-group species, with larger nests occupied yearround and smaller nests occupied during the foraging months (Marikovsky 1963, Talbot 1971, Ito 1973, MacKay and MacKay 1983, Rosengren et al. 1985). Excavations at our study site support this observation, with some nests containing neither brood nor queens in late spring (see

Scherba 1961, Rosengren et al. 1985). This "division of labor" at the scale of the nest may provide the supercolony with temporal flexibility, allowing it to expand when food resources are available in the summer and contract to more insulated nests for protection during the winter months (Rosengren et al. 1985). A long-term advantage of supercoloniality is that multiple nest sites may buffer the colony from catastrophic environmental change, which would decrease the probability of colony extinction (Pamilo and Rosengren 1983).

The plastic nature of *F. rufa*-group species with respect to supercoloniality is a direct consequence of the tendency for workers to accept newly mated queens, and the subsequent use of fission as a primary mode of colony reproduction (Kloft et al. 1973, Ito and Imamura 1974, MacKay and MacKay 1983, Hölldobler and Wilson 1990). Evidence of worker acceptance of queens was clear from the present study as well, with two excavated nests containing numerous de-alated queens deep within nest interiors. Hence supercoloniality in *F. rufa*-group species, with its reliance on asexual reproduction, is analogous to facultative apomixis in plants, in which the colony can suspend outbreeding and independent nest founding whenever environmental circumstances are appropriate: i.e. when sufficient local resources are available and/or dispersal to more distant alternate sites is less profitable (Hölldobler and Wilson 1990). From this argument, we suggest that the mixed-conifer stand at the Lehman site offers relatively stable and abundant food and an abundance of nesting sites for thatching ants in comparison to adjacent forests.

Because of their large population and biomass, *F. rufa*-group colonies can have profound effects on ecosystems in which they live. Potential effects include serving as prey for and competitors of vertebrate species (Gosswald 1990, Haemig 1992), influencing the growth of trees (Rosengren and Sundstrom 1991), and modification of forest soils (Oinonen 1956, Beattie and Culver 1977, Petal 1978). Possibly the greatest documented effect of *F. rufa*-group species is on the abundance and distribution of other invertebrate species, including nest inquilines (Gosswald 1989; William Clark pers. comm.), predators (Cherix and Bourne 1980), and other ant species (Higashi and Yamauchi 1979, Cherix and Bourne 1980, MacKay and MacKay 1982, Savolainen 1989, Puntilla et al. 1994). In addition, the function of *F. rufa*-group species for suppression of insect pest populations has received considerable attention in Asia (Ito and Higashi 1991), in Russia (Grimalski 1959), in Europe (Wellenstein 1952, Laine and Niemela 1980), and in North America (Torgersen et al. 1990). With few exceptions (e.g. *Ips typographus,* Diachenko 1991), *F. rufa*-group species have typically been implicated in population regulation or suppression of lepidopteran (McNeil et al. 1978, Ito and Higashi 1991, Laine and Niemela 1980, Skinner and Whitaker 1981) and sawfly (Baranov 1971) populations.

While other insectivores such as spiders and birds may be capable of reducing forest defoliator populations during their endemic stage and of delaying the onset of defoliator epidemics (Mason 1987), thatching ants may be unique in their power to reduce populations of defoliators in localized areas during the outbreak phase. This power is due not only to their great relative abundance, but also to their propensity to switch to common food as it becomes abundant (Horstmann 1972). Suppression power can be illustrated by estimating the food requirements of the Lehman supercolony and comparing this to an estimate of the food represented by western spruce budworm during outbreak conditions. Although the annual metabolic energy requirement for a supercolony of 56 million individuals is enormous, probably most of this energy is obtained by workers tending aphids and scales for honeydew (Skinner 1980). Thatching ants, however, require insect protein to rear new workers (Skinner 1980). If we assume mean worker dry weight of 2.5mg, a gross production efficiency of 10%, and a mean worker longevity of 3 years (Elton 1977), then the colony of 56 million workers would require about 470 kg dry weight of food annually to replace itself. When this annual food requirement is compared to the potential biomass available during a western spruce budworm outbreak, the power of the supercolony for pest suppression is evident. A stand inventory at the Lehman site conducted in July 1995 indicated 204 stems/ha $\geq$ 15 cm in diameter, and 598 stems/ha < 15 cm diameter. This gives an estimate of 85,390 m^2 of foliage for the study site (Wykoff et al. 1982; Crookston et al. 1990; Crookston 1991). If budworms were to occupy the Lehman site at their maximum observed densities in the Blue Mountains (e.g., 105.6 larvae/m^2 of foliage; Torgersen et al. 1993), a total of 9.02 million budworm larvae

would be present at any given time within the study area, for a total dry weight of 43 kg (4.75 mg average dry weight for 4th instar). This is just 30.4% of the total thatching ant biomass at the site, and just 9.0% (43/470kg) of the total estimated food requirement of the thatching ant supercolony for a single year.

While these figures illustrate the potential for thatching ants to control outbreak budworm populations, no one has experimentally demonstrated pest suppression of this kind. Observations do suggest however, that trees or stands with large populations of thatching ants or red wood ants experience less defoliation than trees or stands lacking them (R. Mason, pers. comm., Laine and Niemela 1980). At Lehman Hot Springs for example, most of the mixed conifer stands adjacent to the study site had suffered heavy defoliation and tree mortality during the recent 10-year outbreak, while most of the trees at the supercolony site itself remained green and relatively healthy.

These observations suggest that where they are common, thatching ants can play an important role in suppression of insect pest populations. Yet for no known reason, species of the *F. rufa*-group are not now common in the mixed-conifer forests of the Blue Mountains. Our 161-km transect across a variety of stand types, conditions, and terrains yielded not one thatching ant colony. Because *F. rufa*-group ants are a potentially important feature of healthy mixed-conifer forests in the Blue Mountains, future research should focus on the factors that explain their low overall numbers and their patchy distribution.

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Using Otoliths and Scales to Describe Age and Growth of Yellowstone Cutthroat Trout in a High-Elevation Stream System, Wyoming

Abstract

Estimates of age and lengths at specific ages of Yellowstone cutthroat trout (*Oncorhynchus clarki bouvieri* Richardson) were made using otoliths and scales. Fish were sampled from 17 high-elevation streams in the Greybull River drainage, Wyoming. Variation in estimates of age within and among three readers were assessed using both structures. Variability among age estimates by individual readers was low for both structures. Estimates using otoliths were significantly less variable than were estimates based on scales both among readers and among estimates by individual readers. Otoliths were more accurate than scales for estimating the correct age of fish. Back-calculated estimates of fish lengths at given ages based on otoliths were significantly less than those based on scales. Hatchery fish grew faster than wild fish at younger ages. Overall, growth of wild fish was slower than in other areas where Yellowstone cutthroat trout are endemic. We predict that if otoliths were used instead of scales to assess age and growth of other trout species in high-elevation streams that similar differences in estimates based on the two structures would be observed.

Introduction

As populations of cutthroat trout (*Oncorhynchus clarki* Richardson) continue to decline (Young 1995), accurate estimates of population statistics, including age and lengths of fish at given ages, become more important to managers attempting to maintain and preserve remaining populations (Summerfelt 1987). Changes in age structure or growth rates can be used to detect environmental changes or ecological conditions influencing growth (Hammers and Miranda 1991). Slow growth may indicate limited food resources, overpopulation, competition with another species, or unfavorable environmental conditions.

Historically, ages of cutthroat trout have been estimated from scale measurements (Brown and Bailey 1952; Laasko and Cope 1956; Averett and MacPhee 1971; Hubert et al. 1987). Recently otoliths have been used (Armstrong 1971; Moring et al. 1981; Lentsch and Griffith 1987; Hubert et al. 1987). However, inconsistencies in age estimates based on these structures have been reported (Hubert et al. 1987; Murray 1994; Campana et al. 1995).

Among cutthroat trout, otoliths reportedly provide better estimates of age than do scales (Hubert et al. 1987), but little research substantiates this claim. In high-elevation systems, scales are thought to yield inaccurate estimates of age because annuli may not form the first year due to late spawning and the short growing season (Brown and Bailey 1952; Alvord 1954; Bulkley 1961; Averett and MacPhee 1971). Also, in trout older than 3-5 years, scales become difficult to interpret because annuli are in close proximity to each other, and scale erosion and re-absorption may obliterate annuli (Alvord 1954).

Yellowstone cutthroat trout (YSC; *O. c. bouvieri*) occupied the largest geographic range among the non-anadromous subspecies of cutthroat trout (Varley and Gresswell 1988), but drastic reductions in their distribution have generated concern about the preservation of genetically pure YSC. Hybridization with and displacement by exotic salmonids and habitat destruction (Gresswell 1988) are estimated to have reduced the range of YSC by 90% (Varley and Gresswell 1988) leading to designation of YSC as a "species of special concern—Class A" by the American Fisheries Society and a "sensitive species" by the U.S. Forest Service in the Northern and Rocky Mountain regions. Paramount to planning and initiating management is the need to understand the

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ecology of the remaining populations of YSC. Yellowstone cutthroat trout occur in high-elevation streams (Gresswell 1988; Young 1995) and little information exists on age structure, growth, or survival of these populations. Previous estimates of age and growth of YSC have been obtained using scales (Remmick 1981; Kent 1984; Gulley and Hubert 1985), but the accuracy and precision of these estimates are questionable (Hubert et al. 1987; Murray 1994).

Using otoliths and scales, we estimated age and lengths at specific ages of YSC in 17 high-elevation (2300-3050 m) streams in the Greybull River drainage in Wyoming. Our objectives were to: (1) ascertain the precision of age estimates using scales and otoliths, both among readers and among estimates by individual readers; (2) ascertain whether otoliths and scales yield different estimates of age or lengths at specific ages; (3) describe growth of cutthroat trout in one high-elevation stream system based on features of otoliths and scales; and (4) ascertain whether there was differences in growth between introduced hatchery YSC and wild YSC in the drainage.

Study Area

The Greybull River drains over 2900 km^2 of the eastern Absaroka Mountain Range in northwestern Wyoming. The study area included that portion of the Greybull River drainage within the Shoshone National Forest (Figure 1). Fifty-six perennial tributaries (355 km of total stream length) occur in the 650 km^2 headwater drainage, and 23 of the perennial streams contained YSC in 1994 (Kruse 1995). The Wyoming Game and Fish Department stocked YSC fry in five of the 23 streams (Anderson, Eleanor, Cow, and Venus creek and the upper Greybull River) in 1988. Stocking occurred above barriers (geologic structures at least 1.5 m high) to upstream migration of fish in streams where no wild YSC were known to occur, except in Venus Creek where hatchery YSC were not isolated from wild YSC by a barrier.

The Greybull River and its tributaries are torrential, high-elevation mountain streams with high channel slopes, unstable substrates, and large fluctuations in discharge from spring to late summer. Elevations of streams in the study range from 2300 to 3050 m above mean sea level. Stream gradients are high, ranging from 0.5 to 25% with a mean of 8.5%. Melting snow dominates the annual hydrograph and results in extremely high spring flows

Methods

Using back-pack electrofishers, YSC were collected from 17 of the 23 streams which contained cutthroat trout (see Figure 1). Two hundred and fifty-nine YSC were weighed (g) and total length was measured (mm). Sagittal otoliths were extracted (Schneidervin and Hubert 1986) from all these fish. From 100 fish, scales were removed from above the lateral line below the insertion of the dorsal fin (Jearld 1983). Otoliths were mounted with epoxy, distal surface up, on a microscope slide (Mackay et al. 1990) and polished with 600-grit sandpaper to clarify annuli. Scales were wet mounted between a coverslip and microscope slide.

Estimates of age based on otoliths and scales from the same 100 fish were made by three independent readers on three separate occasions to determine among- and within-reader variability (Kimura and Lyons 1991; Campana et al. 1995). On each occasion the structures were evaluated in random order. Upon establishing that otoliths were the more reliable aging structure, otoliths from 159 additional YSC were examined three times by all three readers to enhance the array of samples from the Greybull River drainage.

To estimate age of individual YSC, otoliths and scales were viewed on a video screen using the Wyoming Game and Fish Department's Optical Pattern Recognition System (OPRS; Biosonics 1985). Annuli were identified following criteria of Jearld (1983) and Mackay et al (1990). Once each structure had been independently evaluated three times by all three readers, the readers collaborated and agreed on an age. The nucleus, measurement axis, and annuli were shown on the video screen, and the OPRS measured and recorded the radius and distance from the nucleus to annuli for back-calculation of total length at specific ages. Back-calculation is based on the assumption that growth of the aging structure and increase in total length of the fish are directly proportional (Jearld 1983).

Coefficients of variation (CV; Chang 1982; Campana et al. 1995) were calculated to determine within and among reader variation in age determinations. Coefficients of variation for each reader were based on three separate age estimates assigned to a given fish by the reader. Coefficients

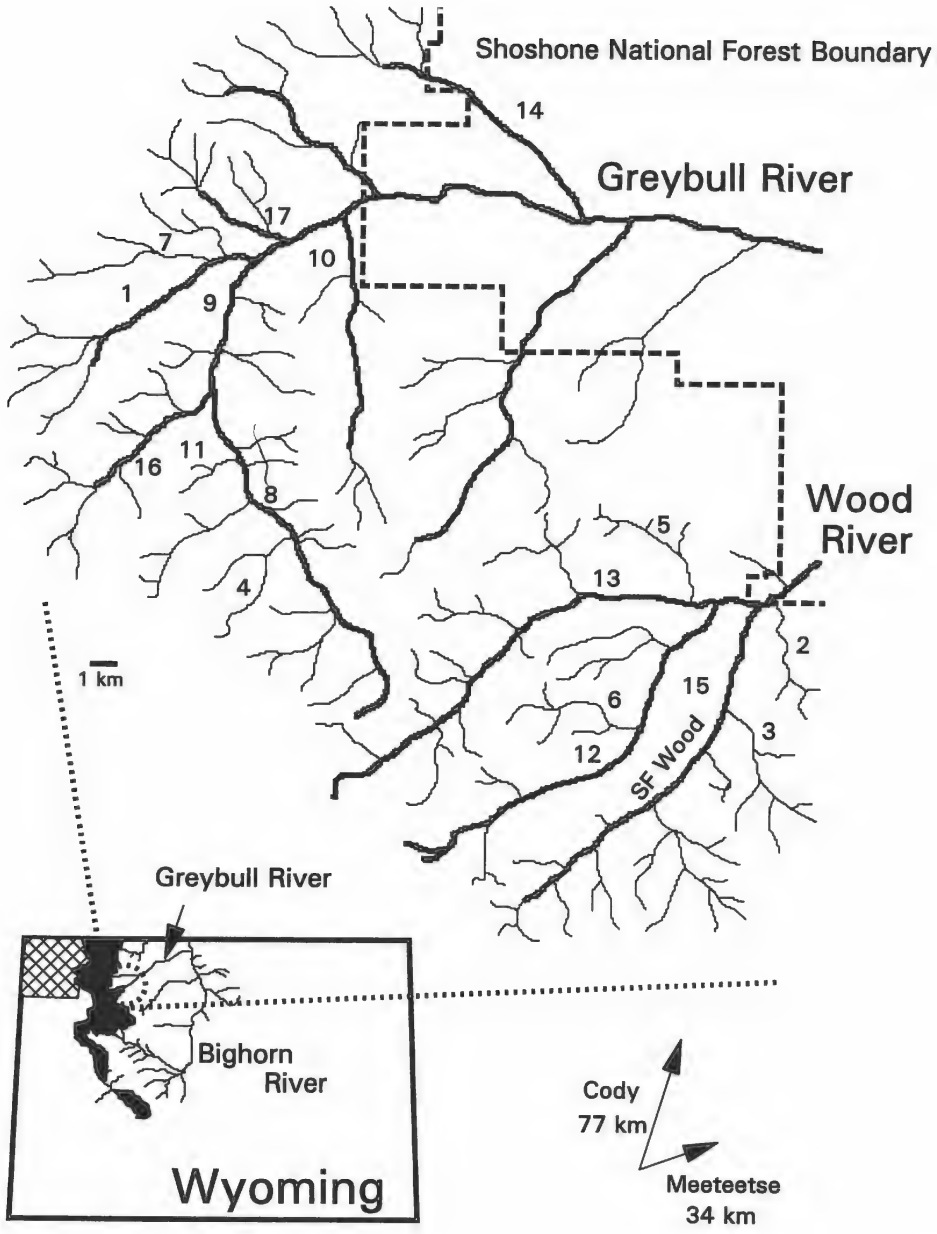

Figure 1. Map showing the location of the Greybull River drainage in Wyoming and location of sampling sites within the drainage. See Table 2 for names of sampling sites corresponding to numbers on the map.

of variation among readers were computed using the mean age (from three readings) assigned to each fish by each reader. One-way analysis of variance (ANOVA; Krebs 1989) was used to detect differences in mean precision (CV) among readers using the same structure and among readings by individual readers using the same structure. Tukey's multiple-comparison test was applied to determine which readers had significantly different CV's.

Age-bias plots were developed to visually assess differences in estimates between readers (Campana et al. 1995). Mean ages determined by one reader were plotted against mean ages determined by a second reader. Pearson correlation coefficients and linear regressions (Neter et al. 1989) between mean ages assigned to otoliths and scales were calculated for each reader.

Mean total lengths at age was used to describe absolute growth of YSC. The direct proportion method was used to back-calculate total lengths (mm) from otolith sections (Lea 1910 *in* Schramm et al. 1992). Back-calculated lengths from scales were computed using the intercept method (Carlander 1982). A correction factor of 42 mm (length at squamation; Brown and Bailey 1952) was used. Two-sample t-tests (Krebs 1989) were used to test for differences in mean lengths at specific ages, based on otoliths, between samples from hatchery-derived and wild populations of YSC.

Validation of age estimates using otoliths and scales was based on a year class of YSC fry stocked in 1988 above barriers to upstream migration of fish in Anderson, Cow, and Eleanor creeks, and the upper Greybull River. In the summer of 1994, this year class was age six. Since there was no evidence of natural reproduction in these streams, the stocked year class provided known-age fish for validation of ageing techniques.

All statistical analyses were performed using SPSS (SPSS 1991). Significance was determined at $P < 0.05$ for all tests.

Results

Coefficients of variation (mean CV) for estimates of age based on otoliths were significantly less than estimates based on scales for all three independent readers (Table 1). No significant differences in mean CV occurred among readers using scales. Reader 2 had a lower mean CV than readers 1 and 3 when using otoliths.

TABLE 1. Mean coefficients of variation within and among three independent readers for scales and otoliths.

	Reader precision		
Reader	Scales (n=100) Mean CV	Otoliths (n=100) Mean CV	P
	Within Reader		
1	13.2[a]	9.55[b]	0.017
2	11.9[a]	5.62[c]	<0.005
3	16.8[a]	8.80[b]	<0.005
	Between Reader		
Among all 3	17.3	8.40	<0.005
1 vs 2	15.1[a]	8.52[b]	<0.005
1 vs 3	21.3[a]	8.52[b]	<0.005
2 vs 3	19.3[a]	9.33[b]	<0.005

[a,b,c] Mean coefficients of variation with the same alphabetical superscript in each category were not significantly different (Tukey's, $P < 0.05$).

The mean CV among the three readers was significantly lower for otoliths than for scales (Table 1). Differences in mean CV between pairs of readers were also significantly lower for otoliths than for scales in all comparisons. No significant differences were found between pairs of readers using the same structure.

Age bias plots revealed differences in age estimates based on otoliths compared to scales, and plots were similar for all readers. For example, the plot of reader 1 versus reader 3 using mean otolith age estimates revealed little difference in ages assigned to otoliths between the two readers (Figure 2, top panel). The regression line did not differ significantly from the 1:1 age ratio reference line indicating little between reader bias. The age-bias plot of reader 1 versus reader 3 for scales revealed differences between the two readers' estimates (Figure 2, middle panel). Reader 3 consistently judged younger fish to be older and older fish to be younger than did reader 1. The bias plot between mean ages assigned to otoliths and to scales by reader 3 revealed that estimates of age using otoliths were consistently higher than those using scales (Figure 2, bottom panel). Readers 1, 2, and 3 had correlations between ages for otoliths and scales of 0.65, 0.67, and 0.46 ($P < 0.0005$ for all cases), respectively.

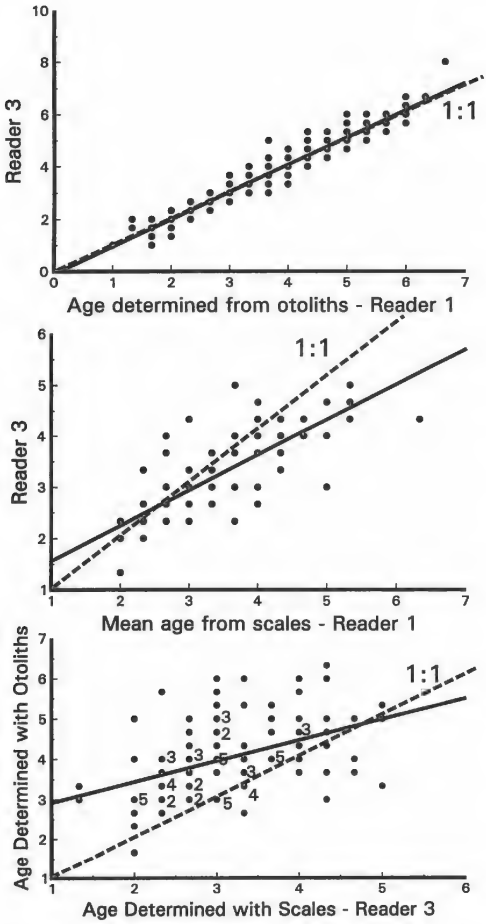

Figure 2. Age bias plots developed from mean ages estimated from otoliths and scales by reader 1 and reader 3. These plots are representative of the relationships in age among all three readers.

Mean back-calculated lengths at specific ages were computed based on otoliths (Table 2). Hatchery fish of given ages estimated from otoliths had significantly greater mean lengths than wild fish at all but age six (Table 3). Scales showed similar results (Table 3). The differences were largest at age one and declined as the fish grew older.

Mean back-calculated lengths at specific ages based on otoliths were less than those based on scales. Back-calculated lengths based on otoliths were 59 mm less than those based on scales at age one for wild fish, and they continued to be significantly less ($P < 0.02$) through age five, although the magnitude of the difference declined with increasing age. At age six there was no significant difference.

Estimates, based on otoliths, of mean ages of 18 YSC from the four streams stocked with hatchery fish revealed that 5- and 6-year-old fish were most abundant (Figure 3). However, the same fish were estimated to be 3- and 4-years old using scales. The known age of the hatchery fish was 6 years.

Discussion

Fisheries scientists use measures of growth, mortality, and age structure to describe fish populations and evaluate management actions. Accurate age data are required to determine these statistics (Schramm and Doerzbacher 1982). Previous studies have suggested that the scale method of age determination is inadequate in both coldwater and warmwater species (Moring et al. 1981; Wigtil 1984; Boxrucker 1986; Hubert et al. 1987; Kozel and Hubert 1987). Otoliths tend to yield higher and more accurate estimates of age for YSC than do scales. We found age estimates using otoliths to be more precise (lower mean CV) and less biased than were estimates based on scales, suggesting that otoliths provide a more reliable and accurate estimate of age of YSC in high-elevation streams. It is probable that YSC in the Greybull River drainage do not reach squamation length (42 mm, Brown and Bailey 1952) during their first summer because of late spawning and a short growing season in the high-elevation system (Alvord 1954; Laasko and Cope 1956; Bulkley 1961; Averett and MacPhee 1971; Lentsch and Griffith 1987), but this does not explain the magnitude of the difference between the mean age estimates using scales (3 to 4 years) and the known age of the fish (6 years).

Age bias plots (Figure 2) revealed results similar to the CV analysis. If estimated ages using scales were 1 year less than corresponding ages from otoliths (simply a function of inadequate length for squamation the first year), we would expect a strong linear relationship. However, while correlation coefficients were significant, they were not strong (all < 0.70), suggesting that there were additional influences on estimates of age based

TABLE 2. Mean back calculated lengths (mm) at specific ages of Yellowstone cutthroat trout from 17 high-elevation streams in the Greybull River drainage, Wyoming, based on otoliths. Numbers in parentheses following stream names indicate location in drainage (Figure 1).

Stream	Age (yr) 1	2	3	4	5	6	N
			Hatchery populations				
Anderson (1)	116	160	206	237	259	274	15
Cow (4)	118	167	251	278	293	304	16
Eleanor (7)	96	136	205	232	256	270	19
U.Greybull (8)	119	188	252	282	300	322	25
			Wild populations				
Brown (2)	58	119	155	158			17
Chimney (3)	68	142	194	233	255	275	16
Deer (5)	73	148	205	240	256		14
Dundee (6)	69	139	197				2
L.Greybull (9)	68	132	196	226	294	319	10
Jack (10)	56	119	167	201			21
Mabel (11)	71	125	181	228	258		1
Md.F. Wood (12)	64	143	195	234	270		13
Wood (13)	72	149	215	252			21
Pickett (14)	85	157	192	212			17
S.F. Wood (15)	67	136	209	255			18
Warhouse (17)	61	128	186	225	244	266	18
			Combination of hatchery and wild fish				
Venus (16)	102	155	222	257	283	268	16

TABLE 3. Mean back-calculated total lengths (mm) at specific ages for hatchery and wild populations of Yellowstone cutthroat trout from the Greybull River drainage, Wyoming, based on otoliths and scales.

Group	Age (yr) 1	2	3	4	5	6	N
			Otoliths				
Wild	67	137	190	228	257	276	183
Hatchery	109	158	224	254	274	287	76
			Scales				
Wild	126	184	233	261	291	324	80
Hatchery	149	214	266	284	292		20

on scales other than the lack of first year squamation. Reader error (Casselman 1987), scale erosion, and obscure annuli (Alvord 1954), may also lead to bias in age estimations based on scales.

Hatchery YSC were longer than wild YSC at young ages, but the difference declined as they grew older. Hatchery YSC may be expected to have faster growth while in a hatchery due to more optimal water temperature and greater food availability than is encountered by wild YSC in the Greybull River drainage. It is important to realize the implications of these differences when assessing growth. If hatchery fish are included with wild fish in samples used for age and growth analysis, estimated length at specific ages will be greater than the actual lengths of wild fish (Table 3).

Comparisons with other cutthroat trout populations (Table 4) were made, but all previous age and growth estimates in published studies were based on scales. Back-calculated lengths at specific ages of wild YSC in the Greybull River drainage were low compared to other cutthroat trout

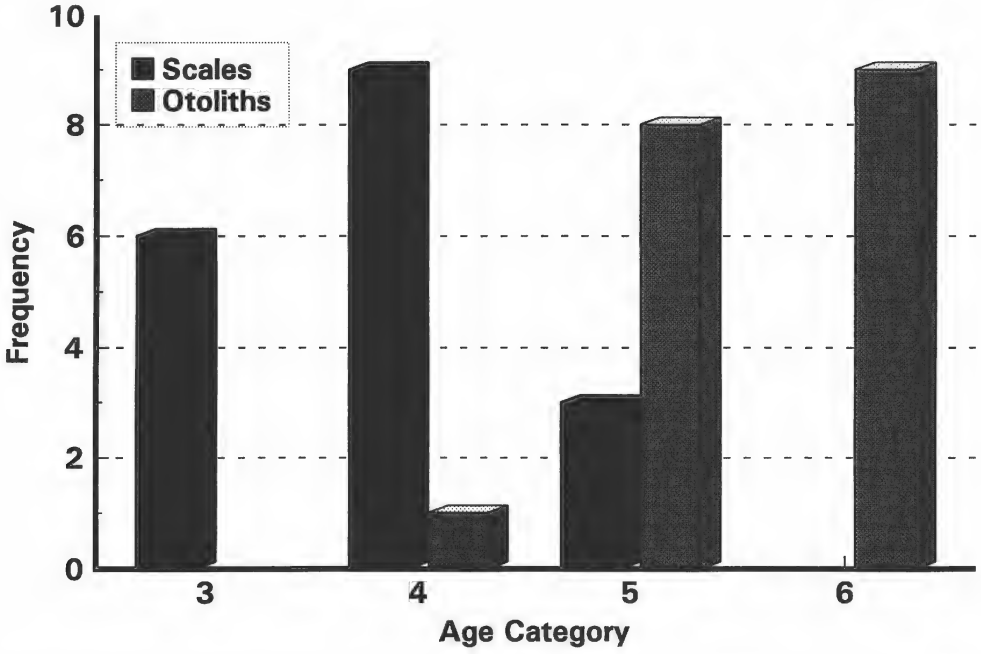

Figure 3. Frequencies of ages determined from otoliths and scales for samples from four study streams stocked with hatchery fish that were 6 years of age at the time of sampling and with no wild fish.

TABLE 4. Mean back-calculated total lengths(mm) at specific ages of cutthroat trout populations throughout the western United States based on scales, and estimates for wild Yellowstone cutthroat trout (YSC) from the Greybull River (GR) drainage, Wyoming, based on otoliths and scales.

	Age (yr)						
Location	1	2	3	4	5	6	Reference
GR scales	126	184	233	261	291	324	This study
GR otoliths	67	137	190	228	257	276	This study
Entire range of YSC	100	180	240	310	370	410	Varley and Gresswell (1988)
Yellowstone Lake	60	140	240	310	350	390	Gresswell(1995)
Montana (mean)	74	132	198	279	330		Carlander (1969)
N.F. Shoshone River, WY	67	134	229	304	375	403	Kent (1984)
Berry Creek, WY	124	186	256	301			Gulley and Hubert (1985)
Blackfoot River, ID	117	213	321	403	442	473	Thurow (1982)
S.F. Snake River, ID	86	184	277	343	410	450	Moore (1984)
Sjhoberg, WY	91	147	218				Remmick (1981)
Bare Creek, WY	79	165	234				Remmick (1981)

populations. Back-calculated lengths based on scales were similar to those reported from other high-elevation cutthroat trout populations in Wyoming (Remmick 1981; Kent 1984). However, the slower growth that we describe based on otoliths is more likely to reflect actual growth in high-elevation mountain streams. Other species of trout in high-elevation montane streams will probably show similar results when aged using otoliths instead of scales.

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Using Mark-Recapture Methods to Estimate Fish Abundance in Small Mountain Lakes

Abstract

The majority of lacustrine fish populations in the western USA are located far from the nearest road. Although mark-recapture techniques are widely accepted for estimating population abundance, these techniques have been broadly ignored for fisheries surveys in remote mountain lakes because of restricted access and associated logistical constraints. In this study, mark-recapture experiments were used to estimate fish population abundance in nine small (< 7 ha) lakes of the North Cascades National Park Service Complex. Fish in the mark sample were collected by angling, fin-clipped, and immediately released; fish were recaptured with variable mesh monofilament gill nets. A single-census Petersen estimator was used to calculate abundance in each lake, and assumptions for unbiased estimates appeared to be satisfied in most cases. Post-release mortality of angler-captured fish was low. The small size of these lakes in conjunction with the brief period of time allotted for each individual experiment apparently reduced the probability of unequal vulnerability and mortality for marked and unmarked fish. Single-census mark-recapture experiments appeared to provide reasonable estimates of population abundance in these mountain lakes. Resulting estimates furnish a substantial increase in information when compared to more ubiquitous assessments of relative abundance, but the logistical requirements are modest. We believe that this technique may useful for survey purposes in other small, remote lakes.

Introduction

Estimates of trout population abundance are often difficult to obtain in lakes located in remote, high elevation areas of the western USA. Fishery managers are frequently required to survey numerous lakes with limited personnel over a relatively short field season. An individual sampling visit to a lake is often of short duration, and there are considerable logistical problems in transporting cumbersome sampling gear. Typically, the status of fish populations in mountain lakes is assessed by gillnetting to obtain estimates of age and size structure and growth, and to provide an index of relative abundance. Although mark-recapture techniques are widely accepted for estimating population abundance, these techniques have been broadly ignored for fisheries surveys in remote mountain lakes because of restricted access and associated logistical constraints.

The purpose of this paper is to describe an application of mark-recapture techniques for assessing trout abundance in small lakes and discuss the general suitability of the method in isolated mountain environments. Angling and gill nets were used to collect fish for mark and recapture samples, and therefore, the method requires a limited number of personnel, an abbreviated sampling period, and easily transported sampling gear.

Methods

Fish population abundance was estimated in nine lakes of the North Cascades National Park Service Complex (NOCA) located in northern Washington, USA. All of the study lakes are relatively small (< 7 ha) and shallow (maximum depth < 10 m). Seven of the study lakes supported reproducing populations of cutthroat trout (*Oncorhynchus clarki*) or rainbow trout (*Oncorhynchus mykiss*). Trout in the other two lakes did not reproduce naturally, and the lakes were stocked with cutthroat trout fry (Liss et al. 1995).

Population abundance was estimated by mark-and-recapture. Fish in the mark sample were collected by angling with barbless lures and flies. Sampling was *direct* (i.e., governed by fishing success; Ricker 1975). Prior to release, individuals were marked by removing the adipose fin or part of the caudal fin (upper or lower tip). To reduce handling time, fish in the mark sample were not measured prior to release. Angling occurred from the shore along the entire perimeter of most lakes and from an inflatable boat; this procedure helped

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to insure mixing of marked and unmarked fish throughout the lake. Injured fish (e.g., those bleeding from gills or tongue) were either released unmarked or sacrificed. Two groups (12 fish in each) were held overnight in enclosures to estimate post-release mortality due to capture and marking.

Fish were recaptured with variable-mesh monofilament gill nets. With one exception, nets were 42 m long with 10.5 m panels of 12.5, 18.5, 25, and 33 mm bar mesh; at Upper Triplet Lake (1991) nets were 34 m long with 11.3 m panels of 13.5, 18.5 and 25 mm bar mesh. Nets were usually set at random locations the day after marking was completed. To minimize reduction in capture efficiency, nets were checked frequently so that fish did not accumulate. Overnight sets were checked the following morning. During recapture sampling net locations were changed often.

Because size-selectivity often varies depending on sampling gear (Ricker 1975), a comparison of mean lengths from fish captured by angling and in gill nets was desired. Results were used to determine the segment of the population to which the abundance estimate applied. Marked fish were not measured prior to release, and therefore, the length distribution of *marked fish* in a pooled recapture sample (from all lakes) was used to represent size distribution for fish captured by angling. Subsequently, recapture samples for individual lakes were partitioned by fish length, and population estimates were limited to size categories encompassed by the pooled sample of marked fish.

A single-census Petersen estimator ($N = (M+1)(C+1)/(R+1)$; Ricker 1975) was used to estimate abundance in each lake. Sampling variance was estimated using Chapman's approximation ($V(N) = N^2(C-R)/(C+1)(R+2)$; Ricker 1975), and coefficient of variation was estimated according to Seber (1982) ($C(N)= 1/(((M*C)/N)^{1/2})$). Upper and lower confidence limits were calculated with Poisson approximations to the hypergeometric distribution (Ricker 1975). Procedures assumed that the proportion of recaptured fish was binomially distributed (equivalent to Poisson distribution of recaptured fish for a given number marked). Individual fish were assumed to behave independently with a constant probability of capture. Equal probability of capture was also assumed for marked and unmarked fish.

Results

Because fish captured by angling were not measured prior to release, the lengths of recaptured fish (R) were used to estimate the size range of fish in the mark sample. Differences were evident in the length-frequency distributions of all fish in the recapture sample and recaptured fish (R) alone (Figure 1). Mean lengths were 209 and 235 mm for all fish sampled and recaptured fish, respectively; the difference was statistically significant (ANOVA; $p < 0.01$). Apparently, angling selected for larger fish than gillnetting, and therefore, abundance estimates were partitioned by fish length so that the assumption of equal probability of capture for marked and unmarked fish would not be violated. Few fish < 170 mm were recaptured in any lake (Figure 1), and in lakes without fish reproduction, fish < 200 mm were infrequent; therefore, estimates for all fish, fish > 170 mm, and fish > 200 mm were calculated separately and compared.

In many lakes estimates for all fish in the population and those restricted to fish > 170 mm (Table 1) did not differ substantially. Smaller fish were apparently underrepresented in both gill-net and angling samples, and thus, mark-recapture estimates underestimated abundance of all fish in reproducing populations. Limiting comparisons to fish > 200 mm substantially reduced abundance estimates when compared to estimates for all fish and for fish > 170 mm. Although confidence intervals were smaller when population estimates were restricted by fish length, statistical bias (because of small sample size; Robson and Regier 1964) occurred in estimates of fish > 200 mm, and sampling variation (as measured by coefficient of variation) increased (Table 1). Therefore, using estimates for fish > 170 mm appeared to provide the most appropriate comparisons of fish abundance among lakes in this study.

Post-release mortality in the two overnight experiments was low. Only 1 of 24 fish died, and that individual was bleeding from the gills when placed in the holding area. Injured fish were not marked at any of the lakes in this study.

Discussion

Using angling and gill-net collections for mark-recapture estimates of fish in remote small lakes had several advantages. At each lake, sampling

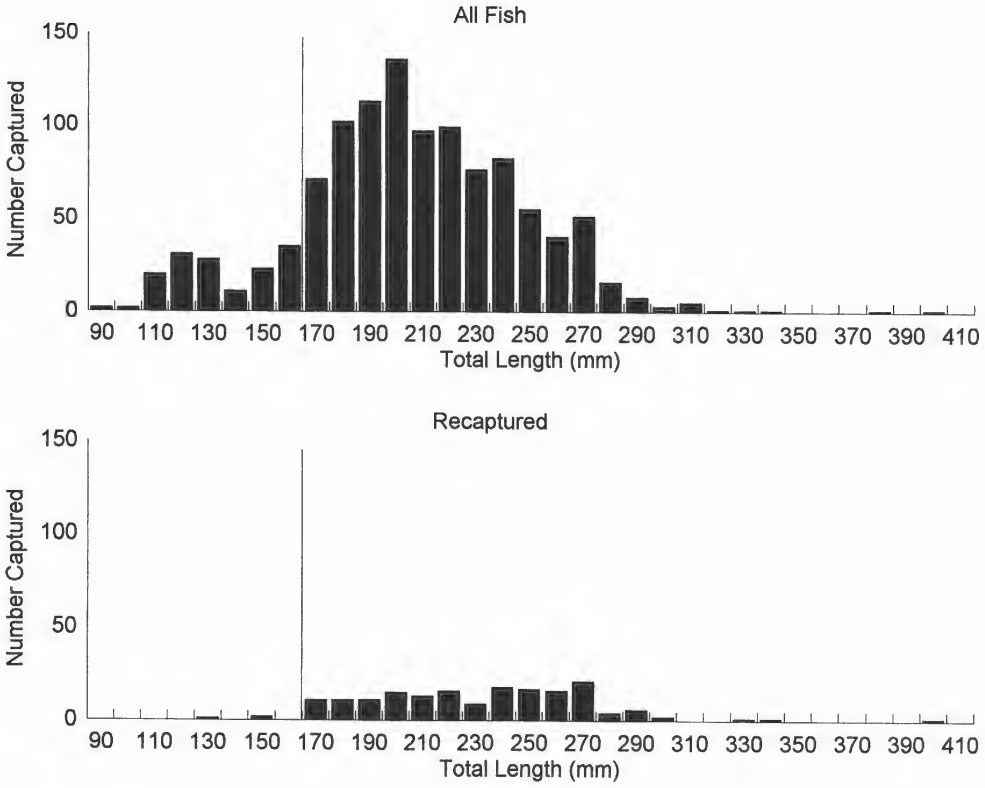

Figure 1. Histograms for lengths (total length) of all fish captured by gillnetting from recapture-samples in lakes of the North Cascades National Park Service Complex, 1991-1993, and for lengths of recaptured fish (R) in the same samples.

gear requirements were limited to several fishing rods and gill nets, an important factor in areas where access is difficult. Initial capture by angling was effective in most lakes, and tests suggested that post-release mortality of marked fish was low. In most cases three people could conduct the survey within 3 d. Precision of population estimates for fish > 170 mm was suitable for long-monitoring studies (White et al. 1982), and estimates appeared to be reasonable for the nine small lakes in this study.

Assumptions associated with the single-census Petersen estimate include equal mortality and vulnerability to capture for marked and unmarked fish. Marks must be retained and remain recognizable throughout the period. Distribution of marked and unmarked fish is assumed to be independent and random, or if not random, subsequent sampling is proportional to the number of fish in different areas. Finally, recruitment should be negligible during the sample period (Ricker 1975).

Previous research suggests that neither of the marks used in this study (adipose and partial caudal fin clips) has adverse effects on survival (Wydoski and Emery 1983), and post-release mortality of marked fish in our enclosure experiments was low. The short period of time between marking and recapture should have reduced the probability of unequal mortality among marked and unmarked fish. It was assumed that no growth or recruitment occurred during this period. Distribution of marked and unmarked fish in the study lakes was unknown; however, all of the lakes were relatively small, and observations suggested that fish moved throughout individual lakes. Gill nets were

Lake	Species[a]	Year	Area (ha)	All Fish								>170mm								>200 mm							
				M	C	R	N	CV	N/ha	LCL	UCL	M	C	R	N	CV	N/ha	LCL	UCL	M	C	R	N	CV	N/ha	LCL	UCL
Reproducing fish																											
LS2	CTT	1992	1.0	101	70	9	724	32	724	402	1448	79	63	7	640	36	640	332	1347	56	47	5	456	42	456	215	1052
MR16	CTT	1993	1.0	50	47	24	98	20	98	67	149	50	44	24	92	20	92	63	140	43	36	21	74	22	74	49	116
Upper Triplet	CTT	1991	1.0	150	77	23	491	21	491	333	755	150	72	23	459	21	459	311	707	150	67	23	428	21	428	290	658
Dagger	CTT	1993	3.6	181	198	14	2415	26	671	411	1156	181	189	14	2305	26	640	392	1104	181	174	14	2123	26	590	361	1017
Kettling	RBT	1993	4.0	310	316	73	1332	12	333	266	417	284	248	69	1014	12	254	201	320	231	107	61	404	13	101	79	129
McAlester	CTT	1992	5.0	210	134	10	2590	30	518	294	999	210	125	10	2417	30	483	274	933	117	45	6	775	38	155	77	339
Rainbow	RBT	1992	6.3	145	208	5	5086	41	807	381	1863	145	167	5	4088	41	649	307	960	116	109	4	2574	45	409	182	1021
Non-reproducing fish [b]																											
LS1	CTT	1992	0.4	34	24	8	97	35	243	130	498	34	24	8	97	35	243	130	498	17	16	4	61[c]	47	152	68	383
Lower Panther	CTT	1992	0.2	28	30	13	64	28	320	195	570	28	30	13	64	28	320	195	570	28	30	13	64	28	320	195	570

[a]CTT = cutthroat trout (*Oncorhynchus clarki*); RBT = rainbow trout (*Oncorhynchus mykiss*)

[b]Fish were removed by intensive gillnetting and angling during 1990, and lakes were restocked with fry in fall 1990 at a density of 313 fry/ha in LS1 and 750 fry/ha in Lower Panther Lake (Liss et al. 1995).

[c]Statistically biased (Robson and Regier 1964)

relocated often during the recapture sample. Furthermore, fish were generally marked and released along the entire shoreline in order to promote mixing of marked and unmarked fish.

Although the use of different types of gear to catch fish for marking and recapture samples may ameliorate non-random distribution of marks or fishing effort (Seber 1982), gear selectivity can introduce systematic bias in mark-recapture estimates (Ricker 1975). Size selectivity occurs with all types of sampling gear, both passive and active (Hayes 1983; Hubert 1983; Reynolds 1983). Although size selectivity is difficult to avoid, effects of this source of systematic bias can be minimized by dividing estimates among two or more size groups or excluding fish near the limits of a given fishing gear (Seber 1982) as we did for lakes in NOCA.

The effects of sampling gear on size distribution can be detected by comparing size distribution of fish in capture and recapture samples. In this study, fish that were captured by angling were not measured prior to release; however, length frequency of fish in the recapture sample suggested differential vulnerability to angling and gillnetting for different length groups in the population. Angling tended to select for larger fish than gill nets. Because smaller fish were underrepresented by both techniques, abundance estimates appeared to be more meaningful when limited to larger fish (e.g., > 170 mm). Fish > 170 mm corresponded to the catchable portion of the fish populations in these lakes, however, and because managers generally focus on the availability of fish to anglers, using angling to mark fish appeared to be appropriate for estimates of the catchable population.

Success of the mark-recapture procedure described here depends on the vulnerability of fish to capture by angling and gillnetting. Dwyer (1990) found that different strains of cutthroat trout could be differentiated by susceptibility to angling. In NOCA, cutthroat trout and rainbow trout initially stocked several decades ago were more vulnerable to both angling and gillnetting than Mt. Whitney rainbow trout that have been stocked in these lakes in recent years. In 1992 attempts to estimate density in two lakes that had been stocked with the Mt. Whitney strain in 1990 failed because a sufficient number of fish could not be captured by angling (W. J. Liss, Oregon State University, unpublished data).

Other methods used to estimate abundance in small lakes have yielded poor results. Kelso and Shuter (1989) employed the removal method (with three different estimators) to estimate total abundance of brook trout (*Salvelinus fontinalis*), lake trout (*Salvelinus namaycush*), and rainbow trout in a small lake (11.7 ha) in north-central Ontario, but variation in catchability throughout the removal period resulted in significant underestimates. The authors cast doubt on the usefulness of the removal technique for lake populations. Cone et al. (1988) used the Jolly-Seber multiple mark-recapture method, but three and possibly four of the six assumptions for this method were violated, and the results were inaccurate.

Bernard et al. (1993) compared direct estimates of abundance of burbot (*Lota lota*) from mark-recapture to an index of abundance based on catch per unit effort in small and moderate-size lakes. If populations of burbot were dense (> 1 adult burbot/ha) and catch rates were high, direct estimates of abundance using mark-recapture experiments yielded more precise estimates than when sampling effort was low, a distinct advantage over using mean catch per unit effort as an index.

Single census mark-recapture experiments appeared to provide reasonable estimates of population abundance in this study, and it may useful for survey purposes in other remote small lakes. In contrast to relative abundance approximations, using a population estimator provides the means to establish confidence limits and promotes among-lake comparisons and temporal trend analysis. Additionally, abundance estimates from mark-recapture experiments provide a level of accuracy and precision suitable for research. The small size of the lakes in this study, in conjunction with the brief period of time allotted for each individual experiment, apparently reduced the probability of unequal vulnerability and mortality for marked and unmarked fish, two important assumptions of the Petersen estimator. Partitioning estimates by size groups is recommended, especially with the combination of angling and gillnetting for collecting fish. Although we were able to accomplish partitioned estimates by crudely approximating the size of fish captured by angling, measuring fish in both the marking and recapture samples is strongly recommended.

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Benthic Invertebrates and Sediment Characteristics in Main Channel Habitats in the Lower Columbia River

Abstract

Benthic invertebrate communities in the Columbia River between the lowermost dam and the upper estuary have been little studied. We describe the abundance of benthic invertebrates and sediment characteristics in main channel habitats in the lower Columbia River and examine the relationships between densities of specific benthic invertebrates and sediment characteristics and water depth. Using a 0.1-m^2 Van Veen grab sampler, we collected benthic samples in seven areas of the river from River Kilometer (RKm) 121 to 211 in April and September 1988 and 1989. Common taxa collected, included Turbellaria, Oligochaeta, the bivalve *Corbicula fluminea*, the amphipod *Corophium salmonis*, Chironomidae larvae, and Ceratopogonidae larvae. Overall, *Corbicula fluminea* and Ceratopogonidae larvae were consistently the most abundant benthic invertebrates. The relationship of benthic invertebrate densities between and within years, months, and areas varied substantially between the six predominant taxa. The effect of water depth and sediment characteristics on benthic invertebrate densities, after accounting for the influence of year, month, and area, varied between the six predominant taxa in this study. Water depth was significant ($P \leq 0.05$) for densities of three of the six taxa, sediment percent silt/clay significant for four, and sediment grain size and percent volatile solids significant for one each. Results from our study are probably applicable to a large area of main channel habitats in the Columbia River downstream from the lowermost dam. Because benthic invertebrates, particularly *Corophium salmonis*, are primary prey for many fishes, the sustained health of benthic invertebrate populations in the lower Columbia River is of concern.

Introduction

The Columbia River downstream from Bonneville Dam (River Kilometer [RKm] 234), the lowermost dam on the river, supports large populations of migrating juvenile salmon (*Oncorhynchus* spp.) and the largest population of white sturgeon (*Acipenser transmontanus*) in the world (DeVore et al. 1995). Studies of the diets of these and other fishes indicate that benthic amphipods and bivalves are often important prey for these fishes. Examples include the tube-dwelling amphipods *Corophium* spp. as primary prey for juvenile chinook (*O. tshawytscha*), coho (*O. kisutch*), and sockeye (*O. nerka*) salmon, steelhead (*O. mykiss*), and juvenile white sturgeon (Kirn et al. 1986; McCabe et al. 1983, 1986, 1993; Muir and Emmett 1988; Muir et al. 1988); and the introduced Asian bivalve *Corbicula fluminea* (= *C. manilensis*) as an important food for juvenile white sturgeon (McCabe et al. 1993).

Despite the importance of benthic invertebrates in the diets of juvenile salmon and white sturgeon, little is known of the distribution and ecology of benthic invertebrates in much of the lower river. Benthic invertebrate communities in the Columbia River downstream from RKm 50 have been studied more than upstream populations (e.g., Higley and Holton 1978; Durkin and Emmett 1980; Durkin et al. 1981, 1982; Emmett et al. 1986; Hinton et al. 1990; Jones et al. 1990). Upstream from RKm 50, benthic invertebrate studies have been limited primarily to short-term or geographically limited studies (e.g., Blahm and McConnell 1979, Blahm et al. 1979, McCabe and Hinton 1990, McCabe et al. 1990). Sanborn (1975) sampled the benthos of four areas in the Columbia River between RKm 29 and 167 in 1973-1974. McCabe and Hinton (1996) described the benthic invertebrate communities and sediment characteristics at 10 dredged-material disposal areas in the lower Columbia River between RKm 55 and 122. McCabe and Hinton's sampling stations were located within about 30 m of the high tide mark on the shore.

From 1987 through 1991, the spawning and early life history of white sturgeon in the lower Columbia River were studied (McCabe et al. 1993, Parsley et al. 1993, McCabe and Tracy 1994). Part of this research involved the collection of benthic invertebrates and sediment samples in eight areas of the lower Columbia River. A portion of

this benthic invertebrate dataset was used in assessing the feeding ecology of juvenile sturgeon in two areas of the river and examining the relationships between juvenile white sturgeon abundance and abundances of two important benthic prey, *Corophium salmonis* and *Corbicula fluminea*, in eight areas (McCabe et al. 1993); however, important specific information about benthic invertebrates and sediment characteristics in the lower Columbia River was not presented.

To elucidate the ecological relationships between the benthos and feeding habits of juvenile salmon, white sturgeon, and other fishes, it is necessary to conduct systematic and long-term benthic invertebrate research throughout the river. To help achieve this goal, we describe the abundance of benthic invertebrate populations in main channel habitats in the lower Columbia River from RKm 121 to RKm 211 using data collected in seven areas. Data collected at one area downstream from RKm 50 are not included because benthic invertebrates have been studied much more in the river downstream from RKm 50 than upstream from RKm 50. We also examine the relationships between densities of specific benthic invertebrates and sediment characteristics and water depth.

Methods

Sampling

Sampling was conducted in seven areas distributed along the lower Columbia River between RKm 121 and RKm 211 in April and September 1988 and 1989 (Figure 1). At each area, designated by RKm, samples were collected along either two or three transects parallel to the shoreline. Transect 1 was closest to the Washington shore, Transect 2 was the middle transect, and Transect 3 was closest to the Oregon shore. In some river sections, only two transects (Transects 1 and 3) were established. Transects selected for benthic invertebrate sampling represented a portion of the total number of sampling transects that was used to determine the range of habitat use by juvenile white sturgeon.

During each survey, five benthic invertebrate samples and one sediment sample were collected at each sampling station with a 0.1-m^2 Van Veen grab sampler (Word 1976). Two sampling stations about 185 m apart were established along each transect. When practical, each benthic invertebrate sample was sieved through a 0.5-mm screen in the field and the residue preserved in a buffered formaldehyde solution (≥4%) containing rose bengal, an organic stain. If it appeared that most of the material would not wash through the sieve, the entire sample was preserved and sieved at a later time. Prior to sorting, all samples were washed with water and preserved in a 70% alcohol solution. Each benthic invertebrate sample was sorted and the invertebrates were identified to the lowest practical taxon and counted. Sediment samples were analyzed for sediment grain size, percent silt/clay, and percent volatile solids by the U.S. Army Corps of Engineers (North Pacific Division Materials Laboratory, Troutdale, Oregon). Each sediment sample was oven dried at 110°C for 24 h, then sieved. Hydrometer analysis was performed if more than 5% of the sample passed through a #230 sieve. Percent volatile solids were determined by weighing an oven-dried sample, then heating the sample in a muffle furnace at 600°C for 1 h. The sample was weighed before and after being placed in the muffle furnace, and the difference between the two weights was used to calculate percent volatile solids. The depth at each sampling station was measured using an electronic depth sounder; all depths were later standardized by converting them to mean lower low water (MLLW).

Data Analysis

Benthic invertebrate data were analyzed by individual sampling station and by combining stations in an area. Information calculated for each station included the number of taxa/categories and mean and standard deviation (SD) of the density (number/m^2) for each taxon/category and total invertebrates. Mean densities of invertebrates from individual sampling stations provided the data for statistical tests.

The relationship between water depth, sediment grain size, percent silt/clay, and percent volatile solids, as compared to year (1988 and 1989), month (April and September), and area were examined using three-factor analysis of variance (ANOVA). The Fisher's Protected Least Significant Difference (FPLSD) multiple comparison procedure was used to compare means from significant F-tests ($P \leq 0.05$) in the ANOVAs (Petersen 1985). The relationship between benthic invertebrate densities and year, month, and area was examined using three-factor analysis of

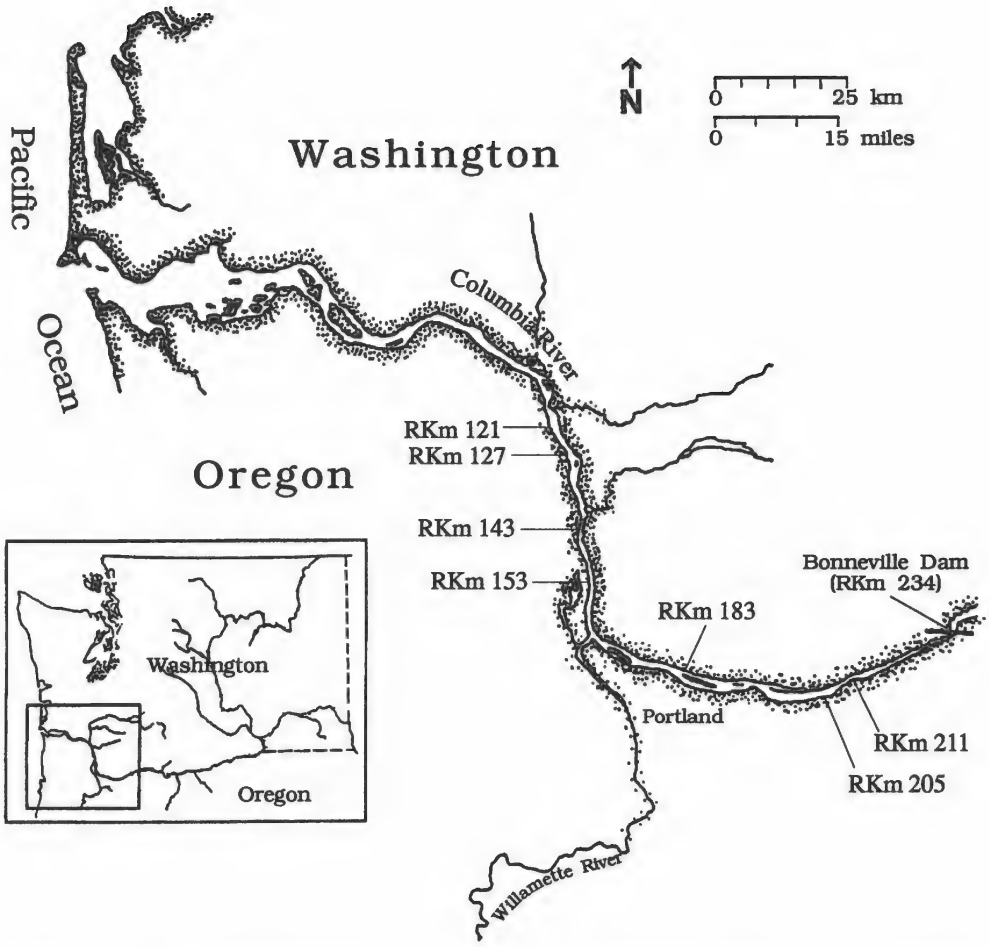

Figure 1. Map of the lower Columbia River showing the seven areas sampled for benthic invertebrates in April and September, 1988 and 1989.

covariance (ANCOVA) and the FPLSD procedure, with water depth, grain size, percent silt/clay, and percent volatile solids as the covariates. Regression equations were developed for significant covariates.

Benthic invertebrate densities were transformed ($\log_{10}$) prior to analyses (Elliott 1977), and sediment characteristics and water depth were transformed ($\sin^{-1}\sqrt{}$) as needed to achieve approximate normality and equal variance of the model residuals.

Results

Water Depth and Sediment Characteristics

Four sediment characteristic values were considered extreme outliers after visual inspection of the data and normality plots: 1) median grain size was 2.22 mm in September 1989 at one station at RKm 205; 2) percent silt/clay was 38.7% in September 1988 at one station at RKm 153; 3) percent silt/clay was 90.4% in September 1989 at one station at RKm 143; and 4) percent volatile

solids was 4.7% in September 1989 at one station at RKm 211. These values were excluded from the analyses.

Significant differences between areas were detected for water depth ($P = 0.004$), median grain size ($P = 0.005$), $\sin^{-1}\sqrt{}$ percent silt/clay ($P < 0.001$), and $\sin^{-1}\sqrt{}$ percent volatile solids ($P < 0.001$). No significant interactions ($P > 0.05$) between year, month, and area or significant differences between years or between months were detected for any of the four variables. RKm 183 had a significantly lower mean water depth than the other areas; depths at RKm 183 averaged less than 7.3 m during all months (Table 1). RKm 143, 183, and 205 had significantly larger mean median grain sizes than RKm 211. Also, RKm 183 had a significantly larger mean median grain size than RKm 121, 127, and 153. RKm 211 had both a significantly higher percent silt/clay and a significantly higher percent volatile solids than the other areas; percent silt/clay and percent volatile solids values averaged $\geq 1.0\%$ during all months (Table 1). Rkm 205 had a significantly higher percent volatile solids than RKm 121, 127, and 183. There were no other significant differences.

Benthic Invertebrates

The number of benthic invertebrate taxa/categories collected in the lower Columbia River ranged from a low of 17 in September 1989 to a high of 20 in April 1989. In both April and September 1988, 19 taxa/categories were collected (Table 2). The number of taxa/categories at individual stations ranged from 4 to 13 in April and September 1988; from 3 to 13 in April 1989; and from 5 to 8 in September 1989. In each area, two to five taxa/categories were numerically dominant during each survey.

Common taxa/categories collected throughout the lower river included Turbellaria (flatworms), Oligochaeta (annelids), *Corbicula fluminea* (bivalve), *Corophium salmonis* (amphipod), Chironomidae larvae (midges), and Ceratopogonidae larvae (biting midges) (Tables 2 and 3). All these taxa/categories were collected in all seven areas during each survey, except for Turbellaria at RKm 205 in September 1988 and Oligochaeta in April 1988 at RKm 205. Overall, *Corbicula fluminea* and Ceratopogonidae larvae were consistently the most abundant benthic invertebrates during the study. Mean densities (by geographic area) of *Corbicula fluminea* ranged from 15 to 733 organisms/m^2. Usually mean densities of *Corbicula fluminea* were less than 500 organisms/m^2 in each area in 1988 and generally less than 300 organisms/m^2 in 1989. Mean densities (by area) of Ceratopogonidae larvae ranged from 48 to 979 organisms/m^2. In 1988, mean densities of Ceratopogonidae larvae were generally less than 650 organisms/m^2 in each area, and in 1989, usually less than 300 organisms/m^2.

For Turbellaria mean densities, there was a significant interaction between year and month ($P < 0.001$) and between year and area ($P = 0.036$), but not between month and area ($P = 0.258$). The mean density of Turbellaria was significantly higher in April 1988 than densities during the other three surveys, which were not significantly different from each other. In 1988, the mean density of Turbellaria at RKm 205 was significantly lower than mean densities at RKm 121, 143, 183, and 211; densities at the other areas were not significantly different from each other. However, in 1989, the mean density at RKm 211 was significantly lower than mean densities at RKm 127, 143, and 183, and mean densities at RKm 153 and 205 were significantly lower than the mean density at RKm 183. Another perspective of the year/area interaction was that at RKm 153 and 211, 1988 had significantly higher mean densities than 1989, whereas there were no significant differences between years for the other areas. Turbellaria density was positively related to water depth after accounting for year, month, and area ($P < 0.001$); however, depth explained only 10% of the variation in Turbellaria density (Table 4).

There were no significant interactions between year, month, and area for Oligochaeta mean densities. Significant differences occurred between months ($P = 0.010$) and areas ($P = 0.019$), but not between years ($P = 0.405$). The Oligochaeta mean density in September was significantly higher than that in April. The mean densities for RKm 183 and 205 were significantly lower than those for RKm 143 and 153. Also, the mean Oligochaeta density at RKm 205 was significantly lower than that at RKm 121. Oligochaeta density was positively related to water depth ($P = 0.025$), grain size ($P = 0.034$), and percent silt/clay ($P < 0.001$) after accounting for year, month, and area; however, these physical characteristics explained only 16% of the variation in Oligochaeta density (Table 4).

TABLE 1. Mean depths (mean lower low water), median grain sizes (GS), percents silt/clay (S/C), and percents volatile solids (VS) at seven sampling areas (RKm-transect) of the lower Columbia River between RKm 121 and 211. Two stations were sampled along each transect.

	April 1988				September 1988				April 1989				September 1989			
RKm-trans.	Dep. (m)	GS (mm)	S/C (%)	VS (%)	Dep. (m)	GS (mm)	S/C (%)	VS (%)	Dep. (m)	GS (mm)	S/C (%)	VS (%)	Dep. (m)	GS (mm)	S/C (%)	VS (%)
121-1	14.0	0.42	0.1	0.7	14.0	0.45	0.0	0.6	15.4	0.58	0.1	0.6	13.6	0.48	0.1	0.7
121-3	11.1	0.32	0.1	0.5	11.0	0.40	0.1	0.6	11.4	0.39	0.1	0.6	10.4	0.42	0.1	0.7
Area	12.6	0.37	0.1	0.6	12.5	0.42	0.1	0.6	13.4	0.48	0.1	0.6	12.0	0.45	0.1	0.7
127-1	20.0	0.64	0.1	0.6	18.0	0.49	0.1	0.6	18.7	0.62	0.1	0.5	17.5	0.58	0.1	0.6
127-2	13.3	0.57	0.1	0.4	11.0	0.41	0.2	0.6	12.0	0.49	0.1	0.6	11.4	0.41	0.1	0.6
127-3	8.8	0.26	0.1	1.0	8.0	0.28	0.1	0.6	9.1	0.32	0.1	0.6	7.3	0.26	0.3	0.6
Area	14.0	0.49	0.1	0.7	12.3	0.39	0.1	0.6	13.3	0.48	0.1	0.6	12.1	0.42	0.2	0.6
143-1	5.9	0.41	0.1	0.6	6.2	0.40	0.4	1.0	5.9	0.34	0.2	0.6	4.0	0.37	0.1	0.8
143-3	15.9	0.56	0.0	0.6	14.5	0.60	0.1	0.7	15.7	0.65	0.1	0.8	14.6	0.70	45.3	1.1
Area	10.9	0.48	0.1	0.6	10.4	0.50	0.2	0.8	10.8	0.50	0.2	0.7	9.3	0.54	22.7	1.0
153-1	19.0	0.65	0.1	0.8	18.7	0.52	0.3	0.8	20.3	0.64	0.0	0.6	18.9	0.61	0.2	0.8
153-2	11.7	0.40	0.0	0.4	12.2	0.34	0.1	0.8	12.8	0.38	0.1	0.7	11.3	0.40	0.1	0.6
153-3	5.9	0.40	0.3	0.6	5.8	0.22	19.4	2.1	5.6	0.36	<0.1	0.6	4.3	0.38	0.6	0.7
Area	12.2	0.48	0.1	0.6	12.2	0.36	6.6	1.2	12.9	0.46	<0.1	0.6	11.5	0.46	0.3	0.7
183-1	7.6	0.86	0.0	0.7	7.2	0.58	0.1	0.6	7.5	0.79	0.1	0.7	6.9	0.94	0.1	0.7
183-3	6.9	0.46	0.1	0.5	5.8	0.40	0.1	0.5	6.7	0.39	0.1	0.6	5.6	0.36	0.1	0.7
Area	7.2	0.66	<0.1	0.6	6.5	0.49	0.1	0.6	7.1	0.59	0.1	0.6	6.2	0.65	0.1	0.7
205-1	8.7	0.28	0.2	0.7	6.5	0.28	0.1	0.5	9.4	0.30	0.2	0.7	6.1	0.26	0.1	0.4
205-3	17.2	0.42	0.0	1.1	14.5	0.82	0.1	1.4	16.8	0.98	0.1	1.4	15.4	1.40	0.1	1.3
Area	13.0	0.35	0.1	0.9	10.5	0.55	0.1	1.0	13.1	0.64	0.2	1.0	10.7	0.83	0.1	0.8
211-1	14.5	0.64	0.1	1.4	13.9	0.46	0.2	1.0	15.7	0.50	0.1	1.1	13.9	0.57	0.1	2.8
211-2	17.7	0.36	0.2	1.2	16.0	0.39	0.1	1.1	17.4	0.18	0.2	0.8	16.3	0.22	1.8	0.8
211-3	5.9	0.17	4.0	1.7	6.4	0.18	2.8	1.4	6.9	0.17	2.8	1.9	3.5	0.18	2.2	1.5
Area	12.7	0.39	1.4	1.4	12.1	0.34	1.0	1.2	13.3	0.28	1.0	1.3	11.2	0.32	1.4	1.7

TABLE 2. Occurrence of benthic invertebrates in the lower Columbia River between RKm 121 and 211, 1988-1989. Presence is indicated by a "+" and absence by a "0."

Taxon/category	1988		1989	
	April	September	April	September
Turbellaria	+	+	+	+
Nemertea	0	+	+	+
Nematoda	+	0	0	0
Nematomorpha	+	+	+	+
Polychaeta	+	0	0	0
Neanthes limnicola	0	+	+	+
Oligochaeta	+	+	+	+
Hirudinea	0	0	+	0
Bivalvia				
Anodonta spp.	0	0	0	+
Corbicula fluminea	+	+	+	+
Gastropoda				
Fluminicola spp.	0	0	+	0
Juga spp.	0	+	0	0
Ostracoda	+	+	+	+
Isopoda				
Gnorimosphaeroma oregonensis	0	0	+	0
Asellus occidentalis	0	+	0	0
Porcellio scaber	0	+	+	0
Amphipoda				
Gammaridae	+	0	0	+
Corophium spp.	0	0	+	+
Corophium salmonis	+	+	+	+
Corophium spinicorne	+	+	+	+
Ramellogammarus oregonensis	+	0	+	0
Hyalella azteca	0	+	+	0
Arachnoidea (aquatic)	0	+	0	+
Ephemeroptera nymph	+	0	0	0
Odonata nymph	0	+	0	+
Trichoptera larvae	+	+	0	0
Diptera				
Diptera pupae	+	0	0	0
Tipulidae larvae	+	0	0	0
Chironomidae larvae	+	+	+	+
Chironomidae pupae	+	+	+	+
Ceratopogonidae larvae	+	+	+	+
Ceratopogonidae pupae	+	0	+	0
Total number	19	19	20	17

Month and area had a significant interaction for *Corbicula fluminea* mean densities ($P < 0.001$), and there was a significant difference between years ($P < 0.001$). Mean densities of *Corbicula fluminea* in 1988 were higher than those in 1989. In April, mean densities at RKm 121, 127, and 205 were significantly lower than densities at RKm 153, 183, and 211, and the mean density at RKm 205 was significantly lower than that at RKm 143. However, in September, the mean density of *Corbicula fluminea* at RKm 205 was significantly lower than the densities at RKm 121 and 127, and the density at RKm 153 was significantly lower than that at RKm 127. Another perspective of the month/area interaction was that mean densities of *Corbicula fluminea* in September were significantly lower than those in April for RKm 121, 127, and 205, but not significantly different for the other four areas. *Corbicula fluminea* density was significantly related to percent silt/clay

TABLE 3. Mean densities (number/m^2) and standard deviations (SD) of benthic invertebrates collected in April and September of 1988 and 1989 between RKm 121 and 211 in the Columbia River. Less common taxa are included in totals, but are not listed individually. Depending upon the number of transects, generally 20-30 samples were collected at each area.

Area		April 1988		September 1988		April 1989		September 1989	
(RKm)	Taxon/category	Mean	SD	Mean	SD	Mean	SD	Mean	SD
121	Turbellaria	41	68	2	7	19	36	2	5
	Oligochaeta	51	103	117	161	27	44	28	49
	Corbicula fluminea	59	112	480	490	30	37	177	207
	Corophium salmonis	46	86	44	71	4	7	39	48
	Chironomidae larvae	26	37	7	12	10	9	3	7
	Ceratopogonidae larvae	146	126	979	1,003	258	263	318	250
	Total	374	293	1,633	1,533	348	318	570	364
127	Turbellaria	33	82	2	6	27	61	12	24
	Oligochaeta	32	68	306	516	70	251	140	269
	Corbicula fluminea	154	218	320	528	15	18	318	350
	Corophium salmonis	27	39	127	158	1	3	256	332
	Chironomidae larvae	11	13	3	9	7	8	4	8
	Ceratopogonidae larvae	161	161	302	371	238	383	205	201
	Total	420	304	1,065	1,150	358	528	936	565
143	Turbellaria	105	144	1	3	6	13	6	23
	Oligochaeta	149	379	48	57	13	18	15	22
	Corbicula fluminea	198	129	336	378	38	51	91	56
	Corophium salmonis	117	197	11	16	29	86	651	532
	Chironomidae larvae	14	18	2	4	1	3	8	13
	Ceratopogonidae larvae	635	563	323	266	164	228	48	43
	Total	1,218	700	722	530	251	264	844	519
153	Turbellaria	28	45	2	4	2	6	1	2
	Oligochaeta	151	321	619	967	227	546	211	371
	Corbicula fluminea	733	980	107	135	263	489	138	181
	Corophium salmonis	122	226	184	298	54	76	359	663
	Chironomidae larvae	36	67	2	5	5	7	14	23
	Ceratopogonidae larvae	606	780	213	264	228	232	190	196
	Total	1,694	1,527	1,128	1,161	779	935	914	628
183	Turbellaria	9	19	3	7	6	13	3	9
	Oligochaeta	1	2	21	38	1	3	7	14
	Corbicula fluminea	189	148	476	494	90	115	60	84
	Corophium salmonis	5	8	43	56	5	8	8	18
	Chironomidae larvae	5	11	38	59	21	29	7	23
	Ceratopogonidae larvae	472	643	886	941	189	144	291	195
	Total	681	753	1,486	1,285	312	223	380	205
205	Oligochaeta	0	0	20	39	129	291	195	436
	Corbicula fluminea	307	532	371	504	16	37	298	663
	Corophium salmonis	23	29	4	7	13	16	12	20
	Chironomidae larvae	40	142	1	3	2	4	33	48
	Ceratopogonidae larvae	73	45	553	818	161	251	360	216
	Total	450	536	950	1,288	323	518	907	996
211	Turbellaria	31	80	10	20	2	7	1	2
	Oligochaeta	144	228	238	457	321	693	131	122
	Corbicula fluminea	640	813	266	303	70	50	106	164
	Ostracoda	20	60	2	5	2	7	14	39
	Corophium salmonis	116	165	79	113	241	337	141	146
	Chironomidae larvae	33	39	21	38	33	47	32	41
	Ceratopogonidae larvae	349	492	314	349	65	74	143	189
	Total	1,338	1,055	955	657	752	968	574	324

TABLE 4. Regression equations and r^2 values relating benthic invertebrate densities to water depth, sediment grain size (GS), percent silt/clay (S/C), and percent volatile solids (VS) after accounting for year, month, and area. Depth is in meters and grain size is in millimeters. Variables were only included if their coefficients from analysis of covariance were significant ($P \leq 0.05$). Transformations are indicated in parentheses. When the $\sin^{-1}\sqrt{}$ transformation was used, the decimal form of the variable was required for calculation (e.g., 0.01 was used for a percent silt/clay of 1.0%).

		Coefficient				
Taxon ($\log_{10}$)	Constant	Depth	GS	S/C ($\sin^{-1}\sqrt{}$)	VS ($\sin^{-1}\sqrt{}$)	r^2
Turbellaria	-0.242	0.064				0.101
Oligochaeta	-0.548	0.053	1.228	10.755		0.163
Corbicula fluminea	1.335			-3.981	6.513	0.046
Corophium salmonis	1.613	-0.060		5.104		0.089
Chironomidae larvae	1.272					0.000
Ceratopogonidae larvae	1.997			-7.115		0.120

($P = 0.005$) and percent volatile solids ($P = 0.049$) after accounting for year, month, and area. *Corbicula fluminea* density was positively correlated with percent volatile solids and negatively correlated with percent silt/clay; however, these physical characteristics explained only 5% of the variation in *Corbicula fluminea* density (Table 4).

For *Corophium salmonis* mean densities, significant interaction was detected between year and month ($P = 0.033$) and between month and area ($P < 0.001$), but not between year and area ($P = 0.056$). Mean densities in September 1989 were significantly higher than those during the other three surveys, which were not significantly different from each other. In September, mean densities at RKm 183 and 205 were significantly lower than those at the other areas, and the mean density at RKm 211 was significantly lower than that at RKm 127. In April, the mean density of *Corophium salmonis* at RKm 183 was significantly lower than mean densities at RKm 143, 153, 205, and 211, and the mean density at RKm 127 was significantly lower than that at RKm 153. Another perspective of the month/area interaction was that mean densities for September were significantly higher than those for April at RKm 121 and 127, but were not significantly different for the other areas. *Corophium salmonis* density was significantly related to water depth ($P < 0.001$) and percent silt/clay ($P = 0.001$) after accounting for year, month, and area. *Corophium salmonis* density was positively correlated with percent silt/clay and negatively correlated with water depth; however, these physical characteristics explained only 9% of the variation in *Corophium salmonis* density (Table 4).

A three-way interaction between year, month, and area was detected for mean densities of Chironomidae larvae ($P < 0.001$). In April 1988, the mean density of Chironomidae larvae at Rkm 183 was significantly lower than mean densities at RKm 121 and 211. In September 1988, the mean density of Chironomidae larvae at RKm 183 was significantly higher than mean densities at RKm 127, 143, 153, and 205. In April 1989, the mean density at RKm 143 was significantly lower than mean densities at RKm 121, 127, 183, and 211. Finally, in September 1989, mean densities of Chironomidae larvae at RKm 121, 127, and 183 were significantly lower than those at Rkm 205 and 211, and the mean density at RKm 121 was significantly lower than that at RKm 153. Density of Chironomidae larvae was not significantly related to water depth and sediment characteristics after accounting for year, month, and area (Table 4).

There were no significant interactions between year, month, and area for mean densities of Ceratopogonidae larvae. There were significant differences for mean densities of Ceratopogonidae larvae between years ($P = 0.007$) and months ($P = 0.009$), but not between areas ($P = 0.131$). The mean density in 1988 was significantly higher than that in 1989. The mean density of Ceratopogonidae larvae in September was significantly higher than that in April. Density of Ceratopogonidae larvae was negatively related to percent silt/clay after accounting for year, month, and area ($P < 0.001$); however, percent silt/clay explained

only 12% of the variation in Ceratopogonidae larvae density (Table 4).

Discussion

It is often difficult to compare data from benthic invertebrate studies done by different investigators. Frequently, there are differences in samplers, sieve sizes, sampling designs, and analyses used by researchers. Given these caveats, we will generally compare findings from the present study to other large-river benthic invertebrate studies. In our study, we observed benthic invertebrate densities somewhat similar to those reported for the Fraser River, British Columbia, and the Hudson River, New York (Northcote et al. 1976, Ristich et al. 1977). In the mainstem of the Fraser River, Northcote et al. (1976) found that annual densities of benthic organisms (including lamprey ammocoetes) usually averaged about 1,000 organisms/m^2, with seasonal averages generally highest in the spring. Dipteran larvae and oligochaetes were the dominant taxa in the mainstem of the Fraser River. Ristich et al. (1977) observed that densities of benthic invertebrates at freshwater stations in the lower Hudson River generally averaged less than 1,000 organisms/m^2 during the four sampling periods. Dominant taxa in freshwater areas of the Hudson River included oligochaetes, chironomids, and other insect species. In the lower Columbia River between RKm 121 and RKm 211, benthic invertebrate densities at individual areas (by survey) often exceeded 1,000 organisms/m^2 in 1988. However, in 1989, benthic invertebrate densities never averaged more than 936 organisms/m^2. Overall, *Corbicula fluminea* and Ceratopogonidae (Diptera) larvae were consistently the most abundant benthic invertebrates in the benthos of main channel areas of the lower Columbia River (Table 3).

Our comparisons of benthic invertebrate densities by area, month, and year highlight the temporal and spatial variabilities in benthic invertebrate populations in the lower Columbia River. Other studies of benthic invertebrates in the lower Columbia River have produced similar findings (e.g., Hinton et al. 1995, McCabe and Hinton 1996, McCabe et al. 1996). For example, McCabe et al. (1996) observed that densities of *Corbicula fluminea* and Ceratopogonidae larvae were significantly different ($P < 0.05$) between surveys and areas in a study conducted near RKm 70 and 73, and *Corophium* spp. densities were significantly different between surveys ($P < 0.05$).

Results from our regression analysis indicated that the density of *Corophium salmonis* was negatively correlated with water depth and positively correlated with percent silt/clay (Table 4). Similarly, McCabe and Hinton (1991) observed that mean densities of *Corophium salmonis* at shallow-water stations (2-5 m deep) at RKm 153 from June through September 1990 frequently exceeded 1,200 organisms/m^2, whereas at nearby channel areas (11-21 m), mean densities of *Corophium salmonis* never exceeded 355 organisms/m^2. McCarthy (1973) observed that *Corophium salmonis* was most frequently found in mud (<0.25 mm), although it also lived in coarser sediments. Hinton et al. (1995) and McCabe and Hinton (1996) noted significant ($P < 0.05$) regression relationships between median grain size and *Corophium* spp. density. In both studies, there was a negative correlation between median grain size and *Corophium* spp. density.

In our study, the density of *Corbicula fluminea* was negatively correlated with percent silt/clay and positively correlated with percent volatile solids (Table 4). In a laboratory and field-laboratory study, fine sand (predominantly between 0.25-0.70 mm particle size in the laboratory and 0.35-0.60 mm in the field-laboratory) was the preferred substrate for *Corbicula fluminea*; however, the clam can use a wide range of substrates, from fine sand to coarser material (Belanger et al. 1985). Fine sand was preferred over organically enriched fine sand. Median grain sizes at many of sampling sites in the seven areas we sampled in the lower Columbia River were within the 0.25-0.70 mm range (Table 1).

Higher bottom water velocities in the main channels than in shallow littoral areas, backwaters, and side channels, probably result in less favorable habitat for specific invertebrates, particularly the tube-building amphipod *Corophium salmonis*. The higher water velocities could limit standing crops of benthic invertebrates by periodically scouring them out of the main channel habitats during periods of high river flow. Periodic scouring and disruption of the bottom sediments may also not allow sufficient buildup of detritus and fine material to support high standing crops of benthic invertebrates.

Because the primary focus of our study was juvenile white sturgeon habitat, our benthic

sampling was limited to main channels of the lower Columbia River; consequently, we did not sample a wide range of depths and sediment types. For example, we generally collected no samples in habitats less than 4 m deep. Sampling of a wider range of depths and sediments may have resulted in better regression relationships between densities of benthic invertebrates and water depth and sediment characteristics.

The lower Columbia River is a navigational channel for commercial ships and barges and requires periodic dredging to maintain adequate depths. Dredged material is often disposed of at deep in-water areas in the lower river. Dredging or disposal operations could impact benthic invertebrates in channel areas downstream from RKm 205.

In general, results from our study are probably applicable to a large area of the Columbia River downstream from Bonneville Dam (RKm 234). The main channel habitats that we sampled are representative of a large area of the lower Columbia River between the estuary (RKm 0-75) and Bonneville Dam (see NOAA Navigational Charts 18523, 18524, and 18531). Much of the river in this reach consists of channel habitat with depths frequently exceeding 10 m. In addition, the substrate in most of the Columbia River between the mouth and Bonneville Dam is sand (0.062-<2 mm). Parsley and Beckman (1994) estimated that the predominant substrate in about 99% of this river reach was sand.

A comprehensive benthic invertebrate study of all aquatic habitat types in the lower Columbia River should be conducted to adequately describe the distribution, abundance, and ecology of these organisms. For example, more research should be concentrated on shallow littoral habitats of the lower Columbia River. These shallow areas, which often support higher standing crops of benthic invertebrates than main channel areas, are generally more susceptible to human impacts than the main channel areas. Besides sampling all habitat types, it is important to establish long-term studies of benthic invertebrate populations in the lower Columbia River in order to recognize natural temporal variations. These studies are necessary to determine the effects of man-made and natural perturbations on the benthos in the lower Columbia River. Within the last 18 years, there have been two major oil spills (1978 and 1984) and one natural disaster, the eruption of Mount St. Helens in 1980, which impacted the benthos of the lower Columbia River. Without long-term studies, it is impossible to determine the extent of the effects of such perturbations on benthic invertebrate communities. Because benthic invertebrates, particularly *Corophium salmonis*, are primary prey for many fishes, the sustained health of benthic invertebrate populations in the lower Columbia River is of concern.

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Propagation and Growth of Pacific Yew (*Taxus brevifolia* Nutt.) Cuttings

Abstract

Vegetative propagation techniques for Pacific yew (*Taxus brevifolia* Nutt.) are little known and could be useful for the management of this long-lived understory species whether for conservation, habitat restoration or for the production of Taxol® (paclitaxel), a promising anti-cancer agent. In this study, cuttings from natural stands of Pacific yew on Vancouver Island were used to test three components of a successful vegetative propagation program; nursery culture, rooting success, and shoot growth and orientation of rooted cuttings. Cultural studies showed that Pacific yew cuttings could be effectively propagated but success rates may not meet expectations derived from studies of other *Taxus* species. Rooting studies showed that cuttings from male and female Pacific yew could be rooted equally successfully. No significant differences were found in rooting percentages of parent trees from 6 Vancouver Island populations. Clonal variation in rooting was significant within those populations (87.5% maximum, 6.4% minimum). Shoot growth of rooted cuttings increased from 3.4 cm in the first year after transplanting to 15.7 cm in the second year. All the cuttings had branch-like orientation. Results showed that a Pacific yew conservation program for the Vancouver Island Region based on vegetative propagation of representative genotypes is feasible.

Introduction

Pacific yew (*Taxus brevifolia* Nutt.), having little commercial value in the past, is one species of which little is known about successful nursery propagation techniques. Such information would be useful in the management of this long-lived species which grows slowly and is scattered in the understory of Northwest forests (Busing et al. 1995). In addition, recently Pacific yew has received greater attention due to the clinical success of Taxol® (paclitaxel), a promising anti-cancer drug extracted from the bark. This has raised concern about the exploitation of natural stands by harvesting and the consequent loss of genetic resources (Scher and Schwarzschild 1989). Due to problems with the acquisition and germination of Pacific yew seed (Rudolf 1974), vegetative propagation could be a feasible way to achieve conservation and restoration goals as well as to meet the demand for paclitaxel (Heinstein and Chang 1994). Vegetative propagation has been successfully used in a program of conservation of genetic resources of some medicinal woody plants in Nigeria (Oni 1993).

The success of a Pacific yew vegetative propagation program depends on whether male and female trees from a variety of geographic locations can be effectively propagated, grown and outplanted. But little is known about rooting cuttings of Pacific yew (Mitchell 1992) and studies of rooting in other *Taxus* species have concentrated on ornamental varieties (Eccher 1988). As a result, rooting success of cuttings from natural stands of Pacific yew may not meet expectations. Cultural studies that test rooting methods established for other woody species would be an important first step in the development of a management program based on vegetative propagation (Oni 1993).

Pacific yew is a dioecious species (Bolsinger and Jaramillo 1990) and differences in rooting capacity between male and female trees may reduce the probability of success in a vegetative propagation program. In *Taxus cuspidata* (Japanese yew), a greater percentage of cuttings from female trees rooted than from male trees (Davidson and Olney 1964). In some dioecious species, differences in physiological and morphological traits have been found between males and females (Dawson and Ehleringer 1993). If rooting capacity is one of those traits, vegetative propagation of one sex or the other may be problematic.

Increasing parent tree age and low growth vigor are other factors known to reduce rooting success (Meier-Dinkel and Kleinschmidt 1990, Roberts and Moeller 1978, Libby and Conkle 1966) and cuttings from some individuals may not root at all, particularly if they are over 100 years old (Brix 1974). Pacific yew cuttings from natural stands may be difficult to root because parent trees can often be over 195 years-old and tend to be slow-growing (Busing et al. 1995). Therefore, old

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age and low vigor may combine to reduce rooting success in cuttings of Pacific yew from natural stands. This would tend to compromise the feasibility of a conservation program.

There are also indications that rooting may vary among parent trees from different geographic locations (Ticknor 1969). However, the extent to which environmental factors affect tree vigor and thus rooting is not well understood (Abedini and Marlats 1988, Libby and Conkle 1966). Pacific yew is widely scattered in its distribution (Bolsinger and Jaramillo 1990, Taylor and Taylor 1981). It is found at elevations up to 800 m and over the entire length and breadth of Vancouver Island (Krajina et al. 1982), an area of great climatic and ecological diversity (Green and Klinka 1994). Therefore, propagation of Pacific yew from stressful (e.g. dry or cold) sites may be problematic as a result of poor shoot growth vigor of the parent trees.

Good shoot growth and upright shoot growth orientation of outplanted rooted cuttings will be important if they are to survive in natural stands, particularly on sites where competing vegetation is a problem for seedling establishment. Such sites are common in the Pacific Northwest (Herring and Etheridge 1976) and on Vancouver Island (Koppenaal and Mitchell 1992). Poor shoot growth is characteristic of Pacific yew in natural stands (Busing et al. 1995) and outplanting may not be successful if rooted cuttings also grow slowly. Branch-like form is frequently found in cuttings rooted from woody plants, particularly if the parent trees are old (Meier-Dinkel and Kleinschmidt 1990, Copes 1987, Rolund 1979, Black 1972). Because Pacific yew parent trees in natural stands can be over 195-years-old (Busing et al. 1995), branch-like form of rooted cuttings could be problematic for plantation establishment. In addition, poor shoot growth and branch-like form may lengthen the time needed to produce Pacific yew cuttings suitable for outplanting or hedging and reduce the feasibility of a vegetative propagation program (Thorpe and Harry 1990).

In this study, three elements of a successful program of Pacific yew propagation were investigated: (1) Cultural studies, (2) Rooting studies and (3) Shoot growth and orientation studies. The objectives were to establish basic cultural procedures for propagating Pacific yew and use them to determine whether cuttings from either male or female trees or from different aspects, elevations or latitudes would be difficult to propagate and grow successfully.

Materials and Methods

The following methods were used for both cultural and rooting studies. Branches were collected from the mid to lower crown of mature (bearing pollen or seed) Pacific yew (*Taxus brevifolia* Nutt.) found in natural stands on Vancouver Island. They were bagged in plastic and returned to the laboratory where they were stored at 2°C. All cuttings were made within 10 days of collection. Cuttings were set in a mixture of equal parts of sand, peat and perlite and placed in outdoor propagation boxes (Brix 1974) with bottom heat (20°C) to root. During rooting, high humidity was maintained and the medium was watered regularly.

Cultural Studies

Four basic cultural experiments were conducted. Because of a scarcity of suitable material for cuttings, each used different parent trees (=ortet). In any given experiment, parent trees were from the same geographic location. Equal numbers of cuttings (=ramet) were set in each treatment in each experiment. Rooting was assessed after 5 months by counting the number of cuttings with at least one root and expressing rooting as a percent of the total number of cuttings in that treatment. No statistical tests were conducted on the data. (1) Rooting was compared between cuttings treated with a basal application of Stimroot 3 (Plant Products, Bramalea, Ontario), that contained 0.8% IBA (indolebutyric acid) and untreated cuttings (two parent trees, 48 cuttings from each tree in each treatment). (2) Rooting of short (3 to 5 cm) and long (25 to 40 cm) cuttings were compared to determine the effects of cutting size (two parent trees, 40 cuttings in each treatment). (3) Effects of tree age were investigated by comparing rooting of reproductively immature (four trees) and mature (four trees) Pacific yew (48 cuttings from each tree in each treatment), and (4) Species variation in rooting was compared between cuttings from Pacific yew and English yew (*Taxus baccata* L.) (two parent trees of each species, 48 cuttings from each parent tree).

Rooting Studies

To assess variation in rooting between male and female trees, three sites were selected on which

there were large trees of both sexes. Branches from one of the sites in the montane (800 m) on Vancouver Island were collected in October 1993. Cuttings were set in early November and assessed for rooting 6 months later. Experimental design consisted of four replicates of 150 cuttings (600 cuttings total) from each of three male and three female trees. Branches from the other two sites on southern Vancouver Island were collected in January 1994. Cuttings were set in early February 1994 and assessed for rooting 6 months later. Experimental design consisted of four replicates of 20 cuttings (80 cuttings total) from each of three male and three female trees from each location (6 trees). Rooting percentages (percent of the total number of cuttings in a replicate with at least one root) were transformed (Arcsin) for normality (Zar 1984). Comparisons were based on nested analysis of variance (Zar 1984) and used Tree(sex) as the error term. Planned contrasts (Mize and Schultz 1985) were made between male and female trees (SAS Institute, V6.0, Cary, NC). Means were separated using Tukey's Studentized Range test (HSD; $p<0.05$).

To assess geographic variation in rooting of Pacific yew, branches were collected from six natural stands on Vancouver Island chosen to represent wet and dry (west and east), cool and warm (north and south), and coastal and montane (low and high elevation) sites. Cuttings were set in late November and assessed 6 months later. Experimental design consisted of four replicates of 12 cuttings (48 cuttings total) from each parent tree at each location. Rooting percentages (percent of the total number of cuttings in a replicate with at least one root) were transformed (Arcsin) for normality (Zar 1984). Comparisons were based on analysis of variance (Zar 1984) in which locations were blocked and trees were nested within blocks. Tree(sex*block) was used as the error term. Planned contrasts (Mize and Schultz 1985) were made between north and south, east and west, and low and high elevation sites (SAS Institute, V6.0, Cary, NC). Means were separated using Tukey's Studentized Range test (HSD; $p<0.05$).

Shoot Growth and Orientation Studies

In March of 1994, rooted cuttings from 3 male (n=101) and 3 female trees (n=80) from a single Vancouver Island location (Iron River) were transplanted into styroblocks (PSB 615A, 45cc) in equal parts of peat, sand and vermiculite and placed in a shaded greenhouse. They were fed once weekly with 100 ppm 20-20-20 (Plant Products, Bramalea, Ontario) and watered as required. Height growth was measured in October of 1994 and 1995. Comparisons were based on nested analysis of variance (Zar 1984) and used Tree(sex) as the error term. Planned contrasts (Mize and Schultz 1985) were made between male and female trees (SAS Institute, V6.0, Cary, NC). Means were separated using Tukey's Studentized Range test (HSD; $p<0.05$).

Shoot growth orientation was assessed in October 1995 on the same two-year-old cuttings as were measured for height growth. A protractor was used to measure the shoot growth orientation (90° = vertical). Male and female trees were compared (Table 4) using nested analysis of variance (Zar 1984) with Tree(sex) as the error term (SAS Institute, V6.0, Cary, NC). Means were separated using Tukey's Studentized Range test (HSD; $p<0.05$).

Results and Discussion

Cultural Studies

Rooting hormone (IBA) increased rooting success from 30.6% to 50.0% (Table 1). Similar results have been found using IBA with a number of other yew cultivars (Eccher 1988, Van Hoff 1978, Von Kornya 1976, Wells 1961). The positive rooting response of Pacific yew cuttings to IBA treatment indicated that hormone treatment was important for a successful propagation program. It may even be essential to successfully

TABLE 1. Summary of rooting percentages (± s.e.) in cultural studies. Hormone treatment was 0.8% IBA. Juvenile trees were less than 1 m tall and did not have reproductive structures. Mature trees were more than 5 cm in diameter and bearing pollen or seed.

Experiment	Treatment	% Rooted
Hormone	+ IBA	50.0 (6.3)
	- IBA	30.6 (9.8)
Size	3-5 cm	55.7 (6.5)
	25-40 cm	50.6 (6.8)
Age	Juvenile	70.8 (6.2)
	Mature	48.6 (8.3)
Species	Pacific yew	45.8 (5.3)
	English yew	95.4 (4.2)

root cuttings from some parent trees (Loach 1988), as was found in Douglas-fir (Brix 1974). Long woody cuttings (37 to 42 cm) rooted successfully (50.6%) and at comparable percentages to short (3 to 5 cm) cuttings (55.7%). Successful propagation of long cuttings has also been found in hardwood shrubs (Wainwright and Hawkes 1988) and in *Taxus* (Bell 1975, Wells 1961). Therefore, long cuttings may be used to accelerate a propagation and outplanting program by producing large trees suitable for outplanting in one less year than if short cuttings were used (Bell 1975). This would also be of benefit in the establishment of hedges for paclitaxel production in nurseries.

Cuttings from juvenile trees rooted 70.8% while those from sexually mature trees rooted 48.6% (Table 1). This has been found for a number of other tree species (Meier-Dinkel and Kleinschmidt 1990, Morgenstern et al. 1984, Brix 1974). Rooting cuttings from juvenile trees may therefore provide a more efficient way to produce large numbers of trees for outplanting than if cuttings from mature trees were used (Thorpe and Harry 1990). In addition, field performance may be better in rooted cuttings from juvenile than mature trees (Ritchie 1991). The use of juvenile parent trees would therefore improve the feasibility of both restoration and paclitaxel production programs.

English yew cuttings rooted with higher success rates (95.4%) than cuttings from Pacific yew (45.8%)(Table 1). Interspecific differences have previously been found in rooting of various *Taxus* species and cultivars (Von Kornya 1976, Wells 1961). Therefore, published procedures for vegetative propagation of English yew (Mitchell 1992) may not work as well when they are applied to rooting Pacific yew cuttings. Nursery programs for paclitaxel production may also be more successful if yew species and cultivars other than Pacific yew are used. Many nursery trials have been done to improve rooting percentages of other woody species (Loach 1988) and great gains have been made through such trials (Mendel 1992). Similar experiments will be needed on Pacific yew cuttings if rooting is to meet expectations derived from previous studies of *Taxus*.

Rooting Studies

There were no significant differences in rooting percentages between male and female Pacific yew trees from the three sites selected to test for sex-specific effects (Table 2). In contrast, cuttings from female Japanese yew (*Taxus cuspidata*) rooted with higher success rates than those from male trees but differences were confounded by clonal effects (Davidson and Olney 1964). Significant clonal variation was also seen in this experiment and rooting percentages of individual parent trees ranged from a high of 49.1% to a low of 1.3% (Table 2). Since both male and female trees rooted with equal success, vegetative propagation could provide a viable means for the conservation of Pacific yew from natural stands.

Rooting percentages were not significantly different over the six Vancouver Island sites selected to test for effects of geographic location (Table 3). Rooting percentages varied among the sites from a low of 30.8% to a high of 66.0%.

TABLE 2. Rooting percentages of cuttings from male (M) and female (F) Pacific yews from three Vancouver Island sites.[1] Row Means (± standard error, se) followed by the same letter are not significantly different (Tukey's Studentized Range; HSD, $p \leq 0.05$). Maximum and minimum rooting percentages were selected from means of 6 parent trees at each site.

Site[1]	Sex	% Rooted (se)	Sex	% Rooted (se)	% Rooted	
					Maximum	Minimum
RR	M	15.8 (6.3) a	F	38.3 (4.8) a	46.3	1.3
RP	M	17.5 (3.9) a	F	19.6 (5.7) a	36.3	1.3
IR	M	34.5 (5.4) a	F	19.8 (3.3) a	49.1	6.9

Planned Contrasts	df	MS	F	Pr>F
Male vs Female (RR & RP)	1	0.3921	1.51	0.2536
Male vs Female (IR)[2]	1	0.2276	0.61	0.4801

[1]Abbreviations:RR, Royal Roads; RP, Rocky point; IR, Iron River.

[2]Iron River is tested separately because it is geographically different from the other twoVictoria area sites and because cuttings were set 3 months earlier than the others.

TABLE 3. Rooting percentages of Pacific yew cuttings from six Vancouver Island sites. Number of parent trees (N) from which maximum (Max) and minimum (Min) rooting percentages were selected. Means (± standard error, se) followed by the same letter are not significantly different (Tukey's Studentized Range; HSD, $p \leq 0.05$).

Site	Lat.	Elev.	N	% Rooted (se)	Max.	Min.
Harmac (HA)	49°08'	50m	3	66.0 (8.5)a	87.5	31.2
Haslam Creek (HC)	49°03'	50m	3	59.0 (7.6)a	87.5	6.4
San Juan Creek (SJ)	48°40'	600m	9	59.7 (3.4)a	75.0	25.0
Rooney Lake (RL)	50°21'	350m	2	42.7 (8.7)a	60.4	25.0
Jordan River (JR)	48°32'	150m	3	34.9 (7.5)a	65.0	14.6
Tsitika (TS)	50°14'	400m	6	30.8 (3.6)a	43.8	14.2
Planned Contrasts			df	MS	F	Pr>F
[1]North vs South (cool vs warm)			1	0.5940	2.76	0.1122
[2]High vs Low (montane vs coast)			1	0.0096	0.04	0.8438
[3]East vs West (dry vs wet)			1	0.1829	0.85	0.3674

[1]RL,TS vs JR,HC,HA; [2]SJ vs JR,HC,HA; [3]SJ,JR vs HA,HC,TS

Planned contrasts between wet and dry sites, cool and warm sites, and coastal and montane sites showed that there was no significant effect of geographic location or elevation on rooting despite potential climatic affects on shoot growth and vigour of parent trees. In Eucalyptus, different ecotypes also had rooting percentages that were not significantly different (Abedini and Marlats 1988). Individual Pacific yew parent trees had rooting percentages as low as 6.4% and as high as 87.5%. This could be the result of parent trees being different ages. Increasing age of parent trees has been found to decrease rooting success and increase clonal variability (Meier-Dinkel and Kleinschmidt 1990, Thorpe and Harry 1990, Black 1972) perhaps through its effects on tree vigour (Roberts and Moeller 1978). High variation in rooting among clones has also been observed in *Larix laricina* (Morgenstern et al. 1984) and in Douglas-fir (Brix 1974). As a result, large numbers of cuttings from parent trees across a broad range of sites may be required for a successful conservation program, as suggested by Wheeler et al. (1995). This may limit the number of rooted cuttings that can be produced in a reasonable time (Thorpe and Harry 1990).

Shoot Growth and Orientation Studies

Pacific yew cuttings grew an average of 3.4 cm in the first year after propagation, but in the second year, height growth increased over four-fold to an average of 15.7 cm (Table 4). No significant differences in growth were found between rooted cuttings from male and female trees in either the first or second year after rooting. Clonal variation in growth was significant, particularly in the second year after rooting when the best clone grew 31.2 cm and the poorest grew 9.7 cm. This is in contrast to Pacific yews in natural stands where shoot growth tends to be poor (Busing et al. 1995). There are also indications that rooted

TABLE 4. Height growth (cm) of rooted cuttings from male and female trees from Iron River in the first (1994) and second (1995) years after rooting. Column means (± s.e.) followed by the same letter are not significantly different (Tukey's Studentized Range; HSD, $p \leq 0.05$).

Sex	Parent Tree	Height growth (cm) 1994	1995
Male	1	1.7 (0.2) a	9.7 (0.7) a
	11	4.5 (0.5) b	31.2 (2.6) b
	9	3.4 (0.4) b	11.8 (0.9) a
Female	2	2.5 (0.3) a	14.8 (1.4) a
	4	4.3 (0.4) b	10.2 (1.4) a
	7	4.1 (0.6) b	16.7 (1.4) a
Male (Average)		3.2 (0.4) A	17.5 (1.6) A
Female (Average)		3.6 (0.5) A	13.9 (1.4) A

TABLE 5. Shoot growth orientation (vertical=90°) of two-year-old Pacific yew rooted cuttings. Means (± s.e.) followed by the same letter are not significantly different (Tukey's Studentized Range; HSD, $p \leq 0.05$).

Site[1]	Sex	Age	Parent Trees	No. of Cuttings	Orientation
IR	Male	2	3	101	55.8° (2.4) a
	Female	2	3	80	52.4° (1.5) a

[1]Abbreviation:IR; Iron River

cuttings may not grow as well as seedlings (Ritchie and Long 1986). Planting trials will be needed to test whether good growth rates in the nursery will be carried to the field. All the rooted cuttings had branch-like form (Table 5). No significant differences were found between cuttings from male and female trees and the average angle of shoot growth was 54.1° from horizontal. Branch-like form is not uncommon in cuttings rooted from woody plants, particularly if the parent trees are old (Meier-Dinkel and Kleinschmidt 1990, Copes 1987, Black 1972). This condition would tend to compromise the survival of cuttings planted on sites where competing vegetation is a problem for seedling establishment. Such sites occur frequently in the Vancouver Island Region (Koppenaal and Mitchell 1992). An upright form may be regained in time (Thorpe and Harry 1990, Rolund 1979) and it may be possible to promote it by staking the trees.

Summary and Conclusions

Cultural studies

Pacific yew can be propagated using published techniques for other *Taxus* species but expectations of rooting success may not be met. Further experiments are needed to increase rooting percentages of Pacific yew so that sufficient numbers of rooted cuttings can be produced for a successful conservation program.

Rooting Studies

Cuttings from male and female trees rooted equally well and cuttings from all parent trees from 6 sites on Vancouver Island were successfully rooted. This is an essential element of a vegetative propagation program aimed at genetic conservation and habitat restoration. Significant clonal variation in rooting percentages indicated that some parent trees may be difficult to root and implied that large numbers of cuttings from each tree would be needed for a viable vegetative propagation program.

Shoot Growth and Orientation Studies

Rooted cuttings grew well in the nursery but two years were required to produce trees tall enough to plant. All the clones had branch-like shoot growth orientation and this may be problematic for survival and growth during the outplanting phase of a Pacific yew conservation program. Field trials of Pacific yew rooted cuttings are needed to test whether the good growth rates achieved in the nursery will continue and whether branch-like form is persistent.

The success of vegetative propagation and subsequent good growth rates of rooted cuttings from Pacific yew indicated that genetic resources of natural stands could be conserved using that approach. Studies are now under way to determine the tolerance of Pacific yew to exposure and drought and to measure the success of outplantings on disturbed sites. Those studies will provide further indications of whether a Pacific yew management program based on vegetative propagation is viable.

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Deliberations on Smoldering Propagation of Combustion in Groundlayers of Humic Substances

During a recent trip to the University of Montana and the Intermountain Fire Science Laboratory in Missoula I was handed a reprint of the 1991 article in this journal on smoldering combustion by W.H. Frandsen. Frandsen emphasises the importance of ground level smoldering combustion in forest fire control, in particular the possibility of a smoldering-to-flaming transition in response to a gust of wind. Having had some laboratory experience (Jones et al. 1994, Jones 1996) of the sort of phenomena which Frandsen reports and analyses I have had a few thoughts re the Frandsen work which I wish to share with readers.

For dry peat moss with few if any inorganics, Frandsen reports a burning rate of $\approx$ 7 g hour^{-1} (2×10^{-6} kg s^{-1}). Let us develop a kinetic equation which incorporates this quantity. Calling the mass loss rate (in SI units) m', we proceed along the lines followed by Frandsen and take the combustion to be restricted to a thin burning volume of rectangular cross section 'a' m^2, whereupon:

$$m' = AVexp(-E/RT) \quad kg\ s^{-1}$$

where σ = peat packing density (kg m^{-3})
A = pre-exponential factor (s^{-1})
V = burning zone volume (m^3)
E = activation energy (J mol^{-1})
R = gas constant = 8.314 J K^{-1}mol^{-1}

We note that V is simply a$\times$h, where h is the thickness of the burning zone. Now smoldering combustion is known (Jones 1993) to follow a propagation rate law:

$$v = \alpha/h$$

where v = propagation rate (m s^{-1})
α = thermal diffusivity (m^{2}s^{-1})

and the thermal diffusivity is, by definition:

$$\alpha = k/c\sigma$$

where k = thermal conductivity (W m^{-1}K^{-1})
c = heat capacity (J kg^{-1}K^{-1})

Inserting these substitutions into our original kinetic equation gives:

$$m' = (Aka/cv)exp(-E/RT) \quad kg\ s^{-1}$$

From information given by Frandsen from his experiments it is possible to obtain at least an inkling of the kinetic dependence of the of the peat moss combustion. We first rearrange the above equation to give:

$$A = (m'cv/ka)exp(E/RT) \quad s^{-1}$$

Now we have a value for m', also for 'a', which is given as 28×10^{-4} m^2, and for v, for which Frandsen gives a range of calculated values the mean of which is 2.25 cm $hour^{-1}$ (6×10^{-6} m s^{-1}). Thomas (1992) gives values of thermal properties of a number of humic materials including 'light, dry soil', to which he assigns k and c values of respectively 0.35 W $m^{-1}K^{-1}$ and 840 J $kg^{-1}K^{-1}$, and these values we shall adopt. The temperature T must be $\approx$ 500°C (773 K); this is known from direct temperature measurements in ignition experiments on peat in which subsequent propagation is by smoldering (Jones et al. in press).

Inserting an arbitrary but reasonable value of 100 kJ mol^{-1} for E gives:

$$A = 60\ s^{-1} \text{ to one sig. fig.}$$

The heat flux q at the smoldering zone (Jones and Richards in press) is simply:

$$q = QshAexp(-E/RT) = (Qk/cv)Aexp(-E/RT) \quad W\ m^{-2}$$

where Q is the heat of combustion (J kg^{-1}). Inserting the value of E used and the calculated value of A, together with a value of 15 MJ kg^{-1} for Q and values of the other quantities as used previously, gives a value of 11 kW m^{-2} for q. Now a black body at 773 K will emit radiation at a rate q_b given by:

$$q_b = 5.7\times10^{-8}\times(773)^4 \quad W\ m^{-2}$$
$$= 20\ kW\ m^{-2}$$

This is close to the value calculated for the smoldering combustion allowing approximations made and for the fact that the emissivity will not be unity. This provides evidence that the kinetics estimated herein are indeed approximately correct.

The radiative flux will occur at the leading edge of the smoldering propagation. At the other side of the smoldering zone (of width h as discussed) heat transfer to unburnt fuel is by conduction. As pointed out in the recent standard text by Griffiths and Barnard (1995), it is because of this that smoldering is slow compared to flaming combustion, there being considerable thermal resistance to conduction from the smoldering zone to the previously unburnt fuel elements.

The experimental results reported by Frandsen (1991) have therefore been shown to have a kinetic basis which could be improved still further by refinement of some of the quantities which have gone into the above treatment. For example, the thermal diffusivity of the material could easily be measured directly. Combustion propagation in materials such as peat, whether smoldering or flaming, has a dependence on the heat flux which in turn has a dependence on the Arrhenius parameters A and E. It is the view of this author that incorporation of these into the analysis of relevant experimental data assists in providing a fundamental framework for the discussion of results and their extension to predict behavior under conditions other than the experimental ones.

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The Northwest Salmon Crisis: A Documentary History

Joseph Cone and Sandy Ridlington, eds.,1996, Oregon State University Press ($29.95)

Probably no environmental issue has more consumed the Pacific Northwest than the survival of salmon. The crisis is one not only of ecology, but also of politics, economics, culture and ethics. A huge salmon literature has developed as the dimensions of the problem have spread. Declines in returning salmon have been exceeded only by increases in the number of reports and publications on the problem.

The Northwest Salmon Crisis is not just another salmon book that rehashes the now familiar story of hydropower, hatcheries, habitat destruction and harvest. It is a unique compilation of historical documents and interpretive commentary that illustrate various dimensions of the salmon problem over time. The book creates an historical perspective on the progression of the crisis while it portrays the importance of salmon to the Pacific Northwest as both commodity and metaphor.

Many of the documents are not familiar or easily accessible to non-specialists, and their collection in a single source is a great service to the reader. The documents are accompanied by contemporary commentary provided by some of region's most noted experts in the biological, ecological, legal, cultural and political aspects of salmon. The commentaries add an invaluable perspective to the documents because many ideas that made sense against the political, economic or philosophical background of earlier times are foreign to contemporary readers.

The book is organized in six sections that contain 82 sets of documents from treaties, tribal councils, state and federal agencies, Bureau of Indian Affairs, congressional hearings, courts, commissions, newspapers, trade papers, professional societies and voter pamphlets.

The introductory essay by William Robbins places the interaction of people and salmon on the Columbia River in historical perspective, emphasizing the relatively short period of time over which the river has been radically changed. Section II, "The Exploitation of Nature," maps the development of the non-Indian salmon fishery from the 1850 treaties to the first notes of alarm at productivity declines thirty years later. Section III, "Contending with Technology," contains a wide variety of documents debating the use of technology in fishing gear, dams, irrigation, hatcheries and logging. It is clear that technology is seen as both a problem and a solution: a problem in its contribution to salmon overexploitation or habitat destruction; a solution in the possibilities of salmon enhancement through hatcheries. As the section progresses, the documents reveal a growing realization that the mounting pressures against salmon could not be alleviated through technological means. Nor could better planning a solution, in part because of the large number of interests and the complexity of coordination.

Section IV, "The Indian Experience," covers the history of Indian attempts to maintain their rights to salmon. The documentary evidence establishes that from the time the first treaties were signed, rights to fisheries were central concerns. Throughout the 20th century, Indians have struggled to maintain their reserved rights to fish and protect fish habitat in competition with growing development pressures on rivers and coastal streams. Several court cases instrumental in affirming Indian rights over salmon are summarized in ways that clarify the complicated issues involved.

Section V, "The Accelerating Crisis," addresses the conflicts between ecological limits and economic development. The ongoing argument about limits to growth and carrying capacity is well represented here. Difficulties of balancing the needs of fish and wildlife with commercial uses of habitat are illustrated by the implementation of various laws, state actions, regional coordination, court findings, and the U.S.- Canada Treaty. The growing concern about the status of wild fish and further extinction of many salmon stocks is the basis of a number of documents that clearly communicate a sense of alarm. The contrast between the

earlier technological optimists and the new generation of technological pessimists is marked. On the other hand, no contrast in the public's ability to reach consensus on solutions is evidenced by a comparison of ballot measures from 1908 and 1992. In a theme that resurfaces from time to time, documents proposing regulation through protected areas are presented from 1892, 1959 and 1993.

In the conclusion, "River of Change," William Lang summarizes the building pressures that have flowed toward the current crisis, characterizing the long and persistent progression of the salmon crisis as primarily a human, and moral, crisis.

Overall, *The Northwest Salmon Crisis* portrays the history of human interaction with salmon with a feeling for the context within which decisions were made. The reader can get an overall picture of the problem from the documents provided, or use the documents as a guide to the pursuit of further depth in original sources. The book will be useful to both general and professional readerships, and would be particularly valuable in graduate-level resource management courses.

In its rich historical detail on salmon, *The Northwest Salmon Crisis* paints a more general picture of the American experience with nature. Resource crises are neither new nor rare in America. Crises build over time, and this book shows us exactly how the salmon crisis developed through a 150 year progression. It details a dynamic of crisis development common to many natural resources. Over time, the threads of human overuse, human alarm at declines in productivity, the compounding effects of multiple uses of rivers and streams and human attempts at technological fixes repeat in waves in increasing intensity.

Cone and Ridlington have put together a comprehensive, insightful and educational collection. I strongly recommend reading *The Northwest Salmon Crisis* for its historical perspective, without which there can be no meaningful understanding of the current problems facing us with salmon and other natural resources.

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Principles and Practice of Plant Conservation

David R. Given, 1994, Timber Press, Portland, Oregon ($39.95, hardcover)

Plants, including those that flower and those that do not, are essential to the well-being of life on earth. In recognition of the "fundamental importance of plants in all conservation activities", the World Wide Fund for Nature and IUCN-The World Conservation Union have sponsored this effort to catalogue and summarize the fundamentals of plant conservation biology for members of the conservation community who are not plant experts. David R. Given treats plants as the organisms of interest in some very broad conservation subjects, such as environmental education, economics, and legislation. The heart of his text provides detailed suggestions for managing *ex situ* collections and *in situ* populations of endangered, threatened, and rare plant species. Dr. Given traveled far to find many interesting case studies; he uses them to illustrate a very broad range of material.

The book begins with a chapter on rationales for conserving biodiversity. Most of these arguments will be familiar to anyone in the field: they range from the economic and medicinal value of plants to ecosystem stability, and scientific and intrinsic value. Dr. Given sets the stage for the dual premise that plants, as well as animals, are in urgent need of care, and that our actions as conservationists and/or scientists must be wed to society at large, especially in less industrialized areas. Both themes reoccur throughout the book. He follows with a discussion of the many roads to extinction. Most of these are obvious (and depressing), and are not unique to plants. Nearly all species face habitat destruction and fragmentation; many also face over-harvesting, inbreeding depression, and the combined injurious effects of these factors with competition, disease and predation.

The next five chapters are devoted to the practice of plant conservation biology. This is the strongest and weakest section of the book. Dr. Given begins the section with a chapter on collecting and managing databases of threatened plant documentation. Here he manages a difficult balance: he offers the reader useful, thoughtful, and explicit information without straying into minutiae. Similar praise is due to a systematic description off-site conservation methods (*ex situ* collections of plant materials in botanic gardens, gene banks, seed banks, and clonal collections). The remaining chapters on managing field, or *in situ* plant populations, in the general case, and in the special instances of protected areas and modified landscapes, are more difficult. This is much less a criticism of Dr. Given's style then it is of the state of the occupation. Plant population biologists recognize that plant persistence and recruitment depends on survival through arduous life history stages from seed dispersal, establishment, and growth to production of viable seed. These phases in turn depend, more or less, on a very long list of interactive factors (spatial structure, population genetic structure, susceptibility to environmental stress, disease, herbivores, reaction to invasive species, etc.) that can either make or break a sensitive population. All of these things are described in Dr. Given's book. But without experimentation, we cannot know exactly which life history stages or interactive factors are the most critical to a specific contracting population. This book would have been strengthened by a statement of the problem, because in the future we will need synthetic treatments of plant population management techniques that can help us to identify and ameliorate specific problems for specific populations.

The final chapters on education, legislation, economics, and setting priorities are another strength of this book. Together, they point to the importance of people in shaping and effecting policy decisions. Conservation will not happen without community support. All of our best efforts in practicing plant conservation can be improved with thoughtful attention to the impact of plants and conservation on people's lives. Few will agree to lose income in order to save a plant. Legislation and education can make people aware of the essential resource that plants provide; economic arguments that favor conservation can tilt the balance. These chapters contain a good summary of material that is not usually presented to biologists.

This book should prove instructive for anyone in need of an introduction to plant conservation biology. For some, it may provide far more. I hope it serves to stimulate more active participation in preserving and protecting plants.

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Restoring Diversity: Strategies for Reintroduction of Endangered Plants
Donald A. Falk, Constance I. Millar, and Margaret Olwell (eds.), 1996, Island Press. (Cloth, $39.95; Paper $27.50).

The reintroduction of endangered species is a controversial subject, with vocal opponents at both ends of the political spectrum. From one camp, we might hear the argument that reintroduction is misguided public policy, interfering with the pursuit of human economic development. "If a species is on the path to extinction, why bother intervening?" At the other end of the spectrum, there is a sentiment that reintroduction is "unnatural", and such efforts shunt limited resources away from the preservation of species and their habitat. A corollary of this view is the concern that once reintroduction is sanctioned as a management tool, the imperative to protect existing populations will be undermined. While the debates over plant reintroduction are rarely as emotionally charged as those over animals, the issue is gaining in importance as ecosystems replace individual species as restoration targets. Thus it is timely that "Restoring Diversity" focuses on the issue of endangered plant reintroduction.

It is interesting that the title of the 1993 conference from which this book arose was "Restoring Diversity: is reintroduction an option for endangered plants?" Apparently the conclusion was a resounding "yes", for the resulting volume does not dwell on the debate. While acknowledging the legal and regulatory pitfalls, the mixed success rate of endangered plant reintroduction, and the debate over priorities, the editors and contributors, by and large, accept reintroduction as a necessary component of ecosystem management. Thus, as the subtitle indicates, the focus of the book is on appropriate "strategies for reintroduction."

Although this book originated from a conference, it is much more than a simple collection of presented papers. The three editors have done an exemplary job of organizing and contributing new material to the volume. The first three sections cover diverse aspects of reintroduction strategy. Each section is prefaced by a useful forward, and includes 4 or 5 contributed chapters followed by a case study illustrating the topic of the section. The chapters in the first section entitled "the environmental and policy context for reintroduction" are also the most disparate. Included are an outline of the current status of endangered plants in North America (north of Mexico) (Morse) and a summary of how the US Fish and Wildlife Service interprets and enforces the laws protecting these plants (McDonald). This section also contains two of the most provocative chapters of the book; one on the potential for radical changes in plant conservation strategies as global climate change progresses (Kutner and Morse); another on the challenges of integrating species reintroductions into a landscape context (White). While several subsequent chapters acknowledge the importance of taking a "bioregional" approach, it is striking that none of the case studies described in the book have been conducted in this manner. The section concludes with a sobering report on plant reintroduction in Hawaii (Mehrhoff). Although 87% of transplanted endangered Hawaiian plants have survived to date, the long-term success of these efforts is still highly uncertain. The above chapters succeed in establishing the current (and future?) environmental and political framework in which reintroduction efforts occur.

The second, and largest section of the book covers "the biology of rare plant reintroduction." All of the stages of plant reintroduction are covered, from selecting reintroduction sites (Fielder and Laven) to monitoring (Sutter) and measuring success (Pavlik). Two pivotal chapters cover demographic, genetic, and horticultural aspects of rare plant reintroduction (Guerrant) and issues of dispersal, establishment, and population structure (Primack). I was struck at how difficult it is to apply the many theoretical considerations raised in these two chapters to the "on the ground" studies described elsewhere in the book. For example, from Primack's chapter one learns that that ecological theory performs poorly when confronted with the vagaries of pocket gophers, drought, etc.

The third section focuses on rare plant mitigation, the "destruction of an existing population or parcel of habitat ... in exchange for habitat elsewhere." This is acknowledged to be "the most controversial application of reintroduction and restoration." The reasons for the controversy are revealed in chapters by Howald and Zedler. Howald documents that many mitigation attempts have

been conducted without "adequate baseline information, critical review, performance standards, realistic evaluation of costs, or recognition of the uncertainty of outcome." Not surprisingly, of 41 such translocations, only 5 are given an unqualified "successful" rating. Incidentally, the great majority of the citations in this chapter are unpublished documents and technical reports. It is nice to have a summary of this fairly inaccessible "gray literature". Zedler provides equally depressing results on the elusiveness of creating wetlands that are functionally equivalent from an ecological perspective. However a recurring refrain of this volume is that we cannot afford to be discouraged by "unexpected outcomes" (we are told in the introduction that the term "failure" should be excised from the vocabulary of plant reintroduction). In this upbeat spirit, chapters by Berg and Bean discuss possible alternatives to mitigation via policy and legal changes, while Klatt and Niemann suggest creative partnerships between public and corporate interests to improve the success of current mitigation efforts.

The book concludes with a synthesis of detailed guidelines for endangered plant reintroduction authored by the editors. Although this is intended to serve as a blueprint for future plant reintroduction efforts, many of the prescriptions are acknowledged to be difficult to meet. For example, genetic diversity should be monitored to insure it is adequate to maintain population viability and sustainability. However, even in the best known model systems, we cannot specify how much genetic diversity is enough to meet these goals. Add the uncertainty over future climatic change, and even less is known. The pragmatic advise to obtain baseline genetic diversity data, and then to monitor levels and trends, is probably the best we can do at present. Similar complications exist for determining basic demographic data such as minimum viable population size. The conclusion that the researcher "will have to explore the literature on the target species or congeners and make a series of best guesses..." is not heartening. Fortunately this statement is followed by two pages of guidance through some of the key demographic issues. Despite these difficulties, the guidelines are a valuable resource. In fact, several of the case studies presented throughout the book might have been more successful if the many issues summarized here had been considered and acted upon.

The message of the book seems to be that endangered plant reintroduction is the direction plant conservation is moving. Perhaps it is no coincidence that one of the editors, Donald Falk, has moved from the Center for Plant Conservation, which he founded and directed, to his current position as executive director of the Society for Ecological Restoration! Whether you agree or disagree with this view, the book is essential reading for anyone interested in learning the "state of the art" of plant reintroduction policy and practice.

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Note: I thank Bob Meinke for helpful comments.

The Hoko River Archaeological Site Complex: The Wet/Dry Site (45CA213), 3,000 -1,700 B.P.

Dale R. Croes, Washington State University Press, ($50.00)

Wet sites are increasingly important in Northwest Archaeology. Unlike the far more common "dry" sites, wet sites are water-logged, containing artifacts that normally do not preserve. At their best, dry sites have stone tools, stone-tool-making debris, dense animal bones and tough plant materials. Wet sites can contain woven baskets, mats, twine, hats, and rope; as well as such wooden items as arrow and harpoon shafts, harpoon heads, carvings, clubs, wedges, planks, shavings and on and on. They also often yield a very wide range of economic and ecological data. Fragile bone and floral material preserve in the wet site's anaerobic conditions. In short, wet sites can be extraordinary repositories of information about ancient people and their ecology.

The most famous Northwest wet site is Ozette, a Makah village on the west coast of the Olympic Peninsula. At Ozette, entire houses were suddenly and hermetically sealed by massive mud slides. The Ozette excavations produced an unparalleled picture of the interior of Northwest Coast houses just before contact with Europeans. However, the picture at Ozette is of a single point in time. Hoko River, with wet deposits spanning 400 years, is one of the few, extensively excavated wet sites along the coast with a lengthy, well controlled stratigraphic record. For that reason, among others, the Hoko River Site Complex is extremely important.

The site is on the Hoko River, just upstream of where it enters the Straits of Juan de Fuca on the northwest tip of the Olympic Peninsula. The complex includes two localities, the wet site with its adjacent dry site, the subjects of the monograph reviewed here, and a rockshelter containing deep but dry midden deposits, the topic of a promised second monograph. The wet site is a series of 47 superimposed vegetal mats that formed in a river channel that was subsequently uplifted and eroded, exposing the mats. The wet site deposits span the period between 3000 and 2600 BP. Unlike the Ozette artifacts, which were sealed more or less where they were used or stored, the Hoko River artifacts were discarded. The artifacts and other cultural debris were incorporated into the mats as they formed by being thrown into the stream from the adjacent bank or dropped in from canoes. The dry site is that of the fishing camp where the artifacts in the water-logged deposits were probably used. The major dry site deposits date between 2900 and 2600 BP. A second dry site occupation area some distance from the first dates to ca. 1700 BP.

Excavations were conducted annually from 1977 through 1983, with subsequent excavations in 1985, 1987 and 1989. A preliminary report was issued in 1980 (Croes and Blinman 1980). In addition to the excavations, the project had four other major parts: 1) replication and experimentation with the replicas of tools found at the site; 2) ethnographic work with Makah people to collect information on technology and subsistence; 3) collection of ecological data from the site's catchment area and: 4) simulation modeling of economic changes on the Olympic peninsula during the past 8,000 years based on micro-economic assumptions about human decision making, and using the economic and ecological data recovered from the site and from activities 2 and 3 above. The simulation modeling is reported in Croes and Hackenberger 1988. The work at hand has two goals: to present an integrated, final report on the excavations of the wet/dry site using information from activities 1, 2 and 3; and secondly, to evaluate predictions made on the basis of the simulation model against data generated by the project and other, recent discussions of Northwest Coast economic and social prehistory.

The monograph is divided into six chapters. Chapter One is the introduction and contains the relevant environmental, archaeological and ethnological background information. It begins with a discussion of the project's problem orientation as it was developed through the simulation research and presents the predictions made from the simulation results for prehistoric economic change on the coast. Chapter Two presents a history of the project, including the site's discovery and excavation, summarizes laboratory methods employed and the project's outreach activities to both the Makah, and the general public. Chapter Three contains a more detailed discussion of how the wet/dry site locality was excavated, and presents their stratigraphy and the floral and faunal

materials recovered (virtually all from the wet site, the dry site having poor preservation). The heart of the monograph are Chapters Four, on the perishable artifacts recovered, and Five, which describes the large assemblages of chipped and ground stone tools from the site.

For readers, professional and lay, interested in Northwest Coast material culture, Chapter Four will be of greatest interest. The Hoko River wet deposits produced a great variety of perishables, including two forms of fishhook, basketry, cordage (in prodigious numbers), lines, wooden wedges, grommets, wooden projectile points, box fragments, line floats among others. It also contained wood working debris. These are all thoroughly described, with excellent illustrations. The descriptions are accompanied by discussions of experiments in replicating the tools and using the replicas to see how the tools were used, under what conditions they worked best and how they broke. Special effort was made in replicating and employing replicated fishing tackle, fundamental research given the ancient and central importance of fishing in Northwest economies. Chapter Five, on stone tools, is of equal interest, particularly the sections on the use of microlithic tools (microliths are small stone blades or flakes). The chapter contains an extensive resume of Jeffrey Flenniken's replication experiments on the hafted microlith knives recovered in the wet site. Flenniken's original work (1981) demonstrated that these tools were likely to have been used for butchering fish. These two chapters are significant contributions to Northwest Archaeology, having implications for interpreting the materials from the far more common dry sites. Croes shows, for example, that non-perishable artifacts —what most of us recover in our dry sites—are less the 5% of the total material culture recovered at Hoko River and Ozette. In these Chapters, Croes demonstrates command of his material and of the comparative data.

The monograph concludes in Chapter Six with a presentation of the author's interpretation of the the wet/dry site's function (a fish camp) and a discussion of economic change on the southern Northwest Coast based on the materials recovered from the site and the computer modeling. The functional conclusions are essentially a description of a diorama constructed of the Hoko River fish camp based on the excavations. I will return to the discussion on economic change below.

Much of the monograph is not new. In many ways, particularly in the first three chapters, it is a minor and only slightly updated revision of the 1980 edited, multi-author report. The section on sea level changes, for example, seems to have no citations more recent than 1983, though a lot of relevant research has been published on the subject since then. For some topics, the 1980 report contains more information than does this one. While Chapters Four and Five do have much that is familiar, there is also much that is new. In addition to the new material in these chapters, Croes pulls together discussions that are scattered through several of his papers as well as those of others of the Hoko research team. The section in Chapter One on the simulation research and the relevant predictions about economic change relies very heavily on lengthy quotations from the 1988 paper. There are more very lengthy quotations in Chapter Six from the published works of Croes and others. I found the long quotes aggravating, and feel they reduced the clarity and flow of the discussions. Readers, and the author, would have been better served by fresh restatements of the predictions, their test implications and the project's results. In fact, I think most readers might find both Chapters One and Six difficult to follow without access to the 1988 paper.

Another criticism I have of the text is actually one I would level at many site reports, but is crucial here. In the faunal analyses, the NISP (Number of Identified Specimen) statistic for each faunal taxon present is given, but not the actual skeletal elements. For example, dogfish (*Squalus acanthius*) have an NISP of 243 but there are no data on the particular skeletal elements present (e.g. vertebrae, ribs, pharyngeal arches, etc.) , so the utility of these statistics for other analyses is limited. There is also no description of how the faunal materials were collected so it is difficult to evaluate the NISP figures. For example, are smelt absent from the assemblage because smelt were not taken by the people who fished out of Hoko, or because the excavation's retrieval methods missed the very small bones of these small fish? I raise this issue (of how the fauna are reported) partially because it is a problem in many archaeological site reports but because ecological and economic data are so fundamental to the results of this project that how they are reported affects how others can evaluate and use its results.

Turning to those results, an essential aspect of the analyses is to demonstrate that while the stone tools from the dry site are most similar to stone tools from contemporary sites in the Gulf of Georgia-Fraser Delta region of southern British Columbia, the basketry are most similar to baskets from wet sites on the outer coast of Washington and Vancouver Island. He wishes to show that basketry reflects ethnicity (and thus the people at Hoko were ethnically tied to people to the west) and that stone tools (and presumably bone tools) reflect broad regional economic stages, and their distributions will therefore cut across ethnic boundaries. Commenting on this arguement is beyond the scope of this review , but his methodology is appropriate. Croes relies on cluster analyses, usually an average linkage clustering of a matrix of Jaccard's similarity coefficients based on a matrix of presence/absence data. The outcome of cluster analyses are extremely sensitive to the clustering method used, the coefficient of similarity or difference used, and to the structure of the original data set. Croes typically runs only one such analysis. His results would be strengthened and more convincing if he ran a few different cluster analyses on each data set to see if his clusters are stable across more than one technique.

In his conclusions, Croes argues that the Hoko River data, coupled with the simulation results, supports the view that significant subsistence and economic changes occured across the southern Northwest Coast during the period between ca. 3500 and 2500 BP. These changes included a region-wide shift to a storage based economy, and to an economy with a heavy, primary focus on fish. He modifies earlier his earlier predictions that this intensification of fish focused first on halibut, then on salmon, suggesting rather that it was of whatever fish were locally available. Flat fish are less common in the deposits than predicted by the simulation model. On the basis of the simulation, he emphasizes intensification of shell-fish as the crucial economic change at this time. Shell fish intensification, as marked by the formation of large shell middens, began as early as 6000 BP is some localities, and widely by 5000 BP on much of the coast. What Hoko does demonstrate is that by 3000 BP there existed a sophisticated fishing technology geared to fully exploiting local fish habitats. This suggests that a storage economy was well developed by this time, if not much earlier.

This is not to diminish the fundamental contributions of this monograph to Northwest prehistory: the descriptions of the artifacts recovered from the site, particularly the perishables, and the replication and experimentation in their use by the Hoko River Project team. For this reason alone, the volume belongs in the libraries of any archaeologist working on the Northwest Coast or on wet sites.

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NORTHWEST SCIENCE

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_____. 1970b. Populations of the yellow pine chipmunk, *Eutamius amoenus.* Amer. Midl. Nat. 83:472-488.

Ceska, A., and H. Romer. 1971. A computer program for identifying species group. Vegetatio 20:48-73.

Grizze, J. E., C. F. Starmer, and G. G. Kuch. 1969. Analysis of categorical data by linear models. Biometrics 25:489-504.

Monographs or books

Jennings, H. S. 1906. Behavior of the Lower Organisms. Columbia University Press, New York.

Papers in proceedings or symposia

Ryland, J. S. 1975. Parameters of the lophophore in relation to population structure in a bryozoan community. *In* H. Barnes (ed.) Proc. 9th Eur. Mar. Biol. Symp., Aberdeen University Press, Aberdeen. Pp. 363-393.

Theses, dissertations, personal communications, and articles in press

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Danwiddie, P. W. In Press. Dichotomous key to conifer foliage in the Pacific Northwest. Northw. Sci.

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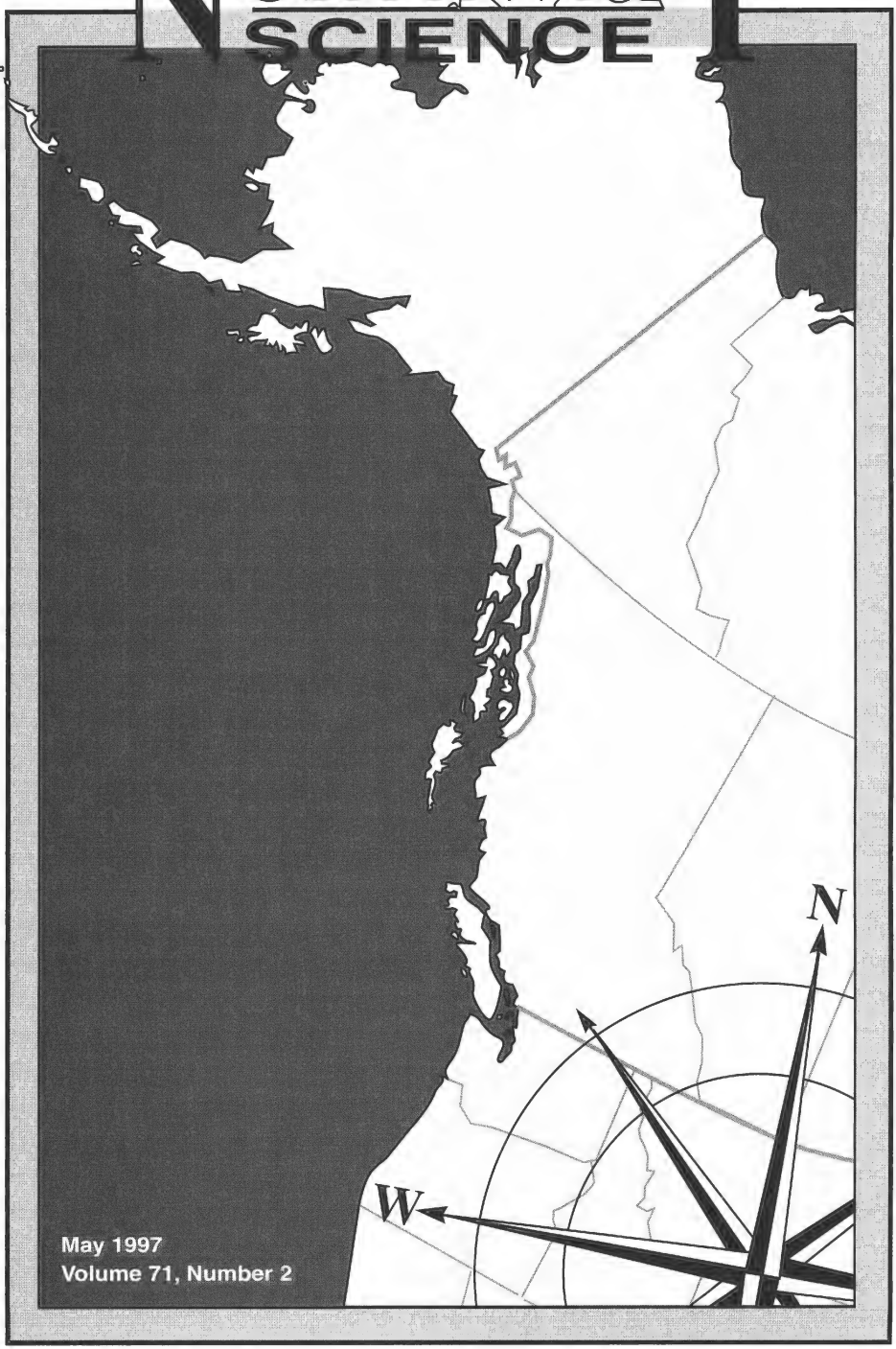
NORTHWEST SCIENCE



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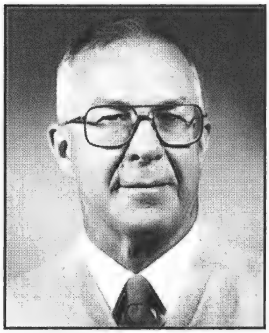
Announcements

Changes in Associate Editors

Dr. Frank Curzon recently resigned from the editorial board of Northwest Science, in addition to retiring from his faculty position at the University of British Columbia. He has served as Associate Editor for Chemistry and Physics since 1983. Dr. Victoria Sturtevant resigned as Associate Editor for Sociology, a position she has held since 1989. The Editor would like to thank both Dr. Curzon and Dr. Sturtevant for their excellent assistance with the review process and for their service to the Northwest Scientific Association.

Honorary Life Member Award

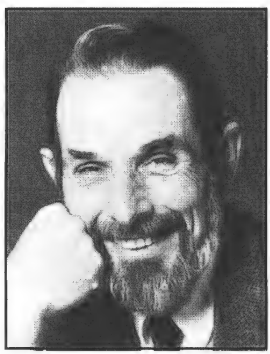


DR. KENNETH HAMMOND, Chair of the Department of Geography at Central Washington University, is this year's recipient of the Honorary Life Member Award. Ken has two BA degrees from Eastern Washington University, an MS from Oregon State University and a Ph.D. from The University of Michigan, all in the area of natural resources or geography. He has been a contributor/editor of 2 major books: *Source Book on the Environment* and *United States Public Policy: A Geographical View.* He has been the recipient of a large number of grants and contracts, the latest of which is a 1.4 million dollar grant to help Native American students in graduate school. He has trained a very large number of graduate students during his many years of service to Central Washington University.

Ken's contributions to the Northwest Scientific Association can be traced to the 1950s when he was introduced to the organization by his mentor, Dr. Frank Schadegg, at a time when the NWSA still held the annual meetings at the Davenport Hotel in Spokane. He has since served as trustee and on a number of committees ranging from "long range planning" to "member recruitment." Most recently he served as President and host of the meetings at Central Washington University.

Ken is known as an exceptional classroom teacher. He is, in fact, a recipient of the Distinguished Teacher Award at Central Washington University. Lesser known is his exceptional service in public education where he has shared his wisdom with farmers and professionals alike, on topics ranging from heritage conservation to western water allocation.

Outstanding Scientist Award



DR. GORDON H. ORIANS, Professor of Zoology at the University of Washington, is this year's recipient of the Outstanding Scientist Award. Dr. Orians has a BS degree from the University of Wisconsin, Madison, and a Ph.D. from the University of California, Berkeley. He has been a member of the Zoology Department at the University of Washington since 1964 and served as Director of the Institute for Environmental Studies for over 10 years of that time.

He has served on a variety of state, regional, and national committees such as the Washington State Ecology Commission, the EPA Ecology Advisory Committee and the Environmental Studies and Toxicology Board. He has published extensively, including major texts such as: *Some Adaptations of Marsh Nesting Blackbirds, Blackbirds of the Americas,* and *Life: The Science of Biology.*

Dr. Orians is a member of the National Academy of Sciences, the AAAS, the AIBS (received the Distinguished Service Award in 1994), the American Ornithologists Union (received the Brewster Award in 1976), The Royal Netherlands Academy of Arts and Sciences, the Organization for Tropical Studies (President 1988-94) and the Ecological Society of America (Vice President 1975-76; President 1994-95).

Dr. Orians has had a long and distinguished career in public education including outstanding contributions in the area of environmental issues and public policy. He is an exemplary member of the scientific community.

Trevor A. Kinley and **Nancy J. Newhouse,** Sylvan Consulting, Box 249, Invermere, British Columbia, V0A 1K0, Canada

Relationship of Riparian Reserve Zone Width to Bird Density and Diversity in Southeastern British Columbia

Abstract

British Columbia forestry guidelines require riparian management areas of 20 to 50 m width between small streams and cutblocks, composed of reserve zones (no timber harvest) and/or management zones (limited timber harvest). Guidelines in Kootenai National Forest, Montana, limit forest harvesting for 30 m adjacent to permanent streams. As one step in providing a basis to assess such guidelines, we compared (1) habitat structure between spruce-dominated riparian forest and pine-dominated upland forest, (2) breeding bird characterisitics (density of detections, species richness, species diversity and species equitability) between riparian and upland forest, and (3) breeding bird characterisitics between riparian reserve zones of various widths (averaging 70, 37, or 14 m wide). The study occurred in the Montane Spruce biogeoclimatic zone of southeastern British Columbia. In relation to upland forest, riparian forest had greater tall shrub and canopy cover, but fewer live trees. Snag density, low shrub cover, and coarse woody debris did not differ at $P<0.05$. The two habitat types did not differ in mean bird species richness per site, but riparian forest had greater species diversity and species equitability, greater density of all species combined, and greater density of three individual species. The density of all birds combined, all riparian-associated birds combined, and three of the four riparian-associated species increased with increasing reserve zone width. Species diversity and species equitability did not differ significantly among treatments.

The widths of riparian management areas required under current British Columbia and Kootenai National Forest guidelines are considerably narrower than the widest category of reserves investigated in this study (70 m). Our data indicate that prescribed riparian management areas under current guidelines will have lower densities of total birds and of riparian-associated birds than if reserves were required to average 70 m in width.

Introduction

Riparian habitats are considered essential for many wildlife species because of high plant and animal productivity, complex habitat structure, proximity to water, and role as movement corridors (Thomas et al. 1979b, Morgan and Wetmore 1986, Bunnell et al. 1992, Bunnell and Dupuis 1993, Naiman et al. 1993, Stevens et al. 1995). In the Montane Spruce biogeoclimatic zone of British Columbia, where this study occurred, approximately 65% of vertebrate species are associated with riparian areas (Bunnell and Dupuis 1993).

The Forest Practices Code of British Columbia requires that forest managers maintain riparian management areas (RMAs) between cutblocks and streams, consisting of riparian reserve zones (RRZs) with no forest harvest and riparian management zones (RMZs) with limited harvest. The width of these zones is variable, depending on a stream's channel width and its value for fisheries or as a domestic water supply. For streams less than 20 m wide, reserve zones vary from 0 to 30 m and management zones vary from 20 to 30 m, for a total of 20 to 50 m (BC Ministry of Forests and BC Environment 1995). The national forest nearest to the study area is Kootenai, in northern Montana. Guidelines for Kootenai National Forest require that permanent streams be buffered by streamside management zones (SMZs) that are generally 30 m wide and in which only limited timber harvesting is permitted (Kootenai National Forest 1994).

In western North America, little riparian research has been specific to conifer-dominated riparian habitats of dry to mesic inland montane regions. However, it is well established that the creation of edge and the ratio of edge to interior forest habitat have significant effects on faunal characteristics (Thomas et al. 1979a, Strelke and Dickson 1980, Kroodsma 1982, Hansson 1983, Kroodsma 1984, Wilcove 1985, Thompson et al. 1992, Faaborg et al. 1993). Recently, several studies have specifically addressed the effects of the width of riparian reserve zones or management zones on bird community characteristics. Narrow reserves generally fail to provide habitat for the complete range of naturally-occurring bird species (Stauffer and Best 1980, Croonquist and Brooks 1993, Spackman and Hughes 1994, Darveau et al. 1995, Gyug 1995), but results differ

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between landscapes. In some situations, no major differences are apparent even over a broad range of riparian reserve zone widths (Smith and Schaefer 1992). Furthermore, McGarigal and McComb (1992) report a case where riparian zones exhibit lower species diversity and density than upland sites. Therefore, it is not clear to what extent current forestry guidelines will maintain the ecological values of riparian habitats of the inland Northwest.

As one step in providing an empirical basis to assess guidelines, we compared (1) habitat structure between riparian and upland forest, (2) breeding bird characterisitics between riparian and upland forest, and (3) breeding bird characteristics between riparian reserve zones of various widths in the Montane Spruce biogeoclimatic zone of southeastern British Columbia.

Methods

This study occurred in the "Dry, Cool Montane Spruce" (MSdk) biogeoclimatic subzone of the Invermere Forest District in southeastern British Columbia (Figure 1) at elevations of 1100 to 1300 m. Mean annual precipitation for the MSdk is 590 mm, with a mean summer temperature of about 8.5°C and a mean winter temperature of about –3.0°C (Braumandl and Curran 1992). Fifteen study sites were established adjacent to streams with channels 1 to 10 m wide, paralleling one side of the stream for 300 m and extending upslope for 100 m. Sites were a minimum of 500 m apart at the closest points. The forested area in each site included riparian forest on historic floodplains and upland forest farther upslope, and was 80 to 140 years old. Sites exhibited complex vegetational patterns, but based on the MSdk classification (Braumandl and Curran 1992), riparian forest corresponded most closely to the "hybrid white spruce - dogwood - horsetail" (*Picea glauca x engelmanni - Cornus stolonifera - Equisetum arvense*) series, and upland forest was most similar to the "lodgepole pine - Oregon grape - pinegrass" (*Pinus contorta - Mahonia aquifolium - Calamogrostis rubescens*) series. Control sites contained only riparian and upland forest, while treatments included recent clearcuts (<1 to 5 years old) at the upslope end. The three treatments were classed as narrow, medium or wide reserve zones, according to the width of forest remaining between the cutblock and the stream (Table 1 and Figure 2). These strips of forest corresponded to RRZs of Forest Practices Code nomenclature, and included both riparian and upland vegetation. Forest on the opposite side of the stream from each site was in a mature, uncut state and was vegetationally similar to the study site. Habitat types in all sites were mapped at 1:1000 scale, based on transects run perpendicular to the stream at 25-m intervals. The forested area of each site was determined using a digital planimeter, then divided by 300 m to yield the mean width of each reserve zone.

Coarse woody debris (CWD) volumes were assessed using the method of Lofroth (1992), and included all pieces ≥10 cm diameter on one 200-m transect per habitat type at 15 sites. Sampling methods for vegetative characteristics were modified from provincial standards (Habitat Monitoring Committee 1990) because the linear nature of our riparian sites and the habitat units within

TABLE 1. Characteristics of 15 riparian study sites in the Montane Spruce zone, Invermere Forest District, B.C., 19939-1994.

Characteristic		Control	Treatment		
			Wide Reserve Zone	Medium Reserve Zone	Narrow Reserve Zone
Sample Size		5	3	5	2
Width of Riparian Forest (m)	Mean (Range)	27 (9-45)	25 (11-44)	21 (13-31)	14 (13-14)
Width of Upland Forest (m)	Mean (Range)	73 (55-91)	45 (29-54)	16 (10-23)	0
Total Width of RRZ (m)	Mean (Range)	—	70 (64-73)	37 (33-43)	14 (13-14)
Width of Cutblock (m)	Mean (Range)	—	30 (27-36)	63 (57-67)	86 (86-87)
Total Site Width (m)		100	100	100	100
Length Parallel to Stream (m)		300	300	300	300
Aspect		2N,2S,1W	1N,2E	3N,2S	1N,1E
Slope (L=<10%; H=>10%)		1L,4H	3H	2L,3H	2L

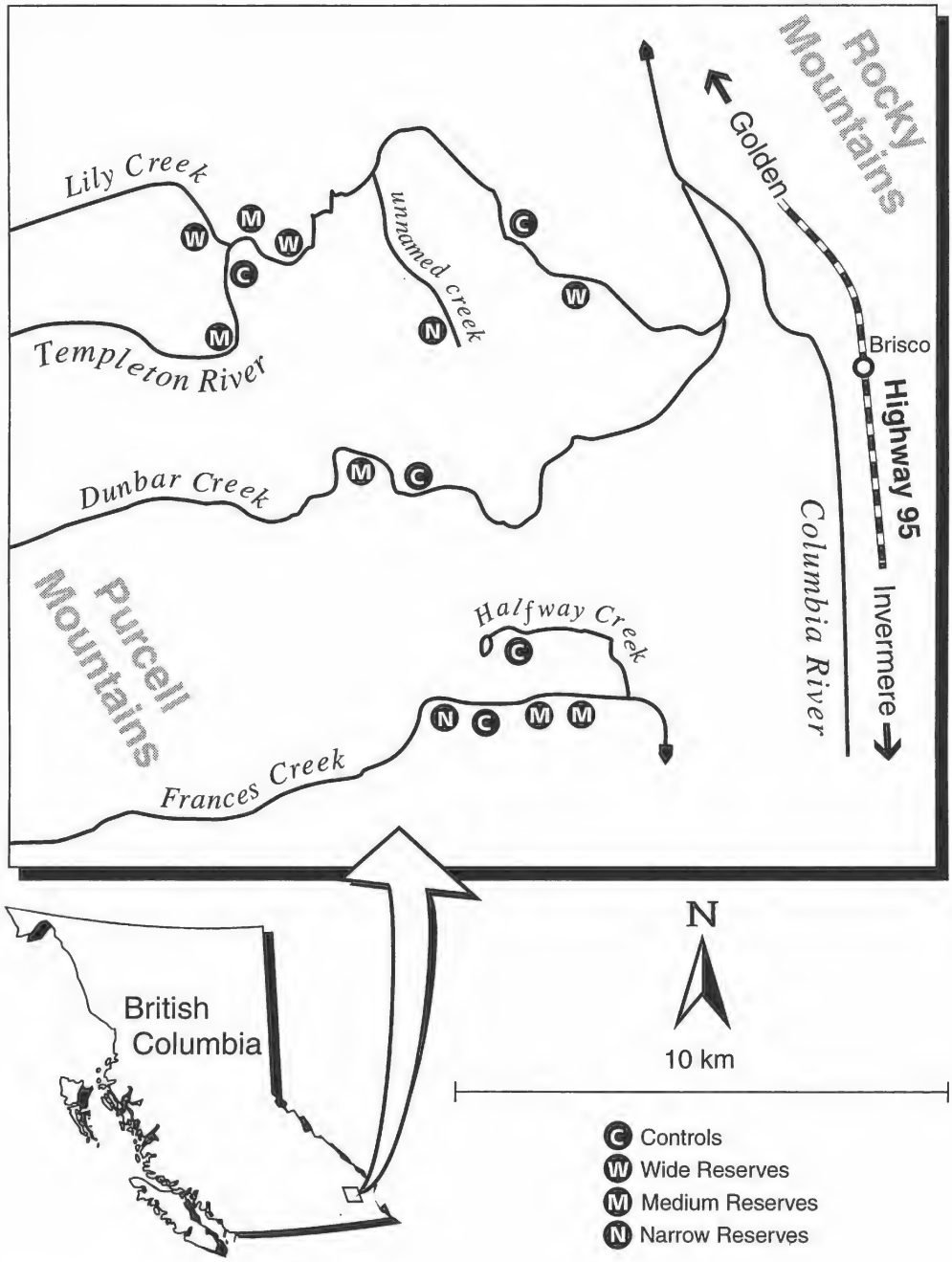

Figure 1. Study area and study site locations.

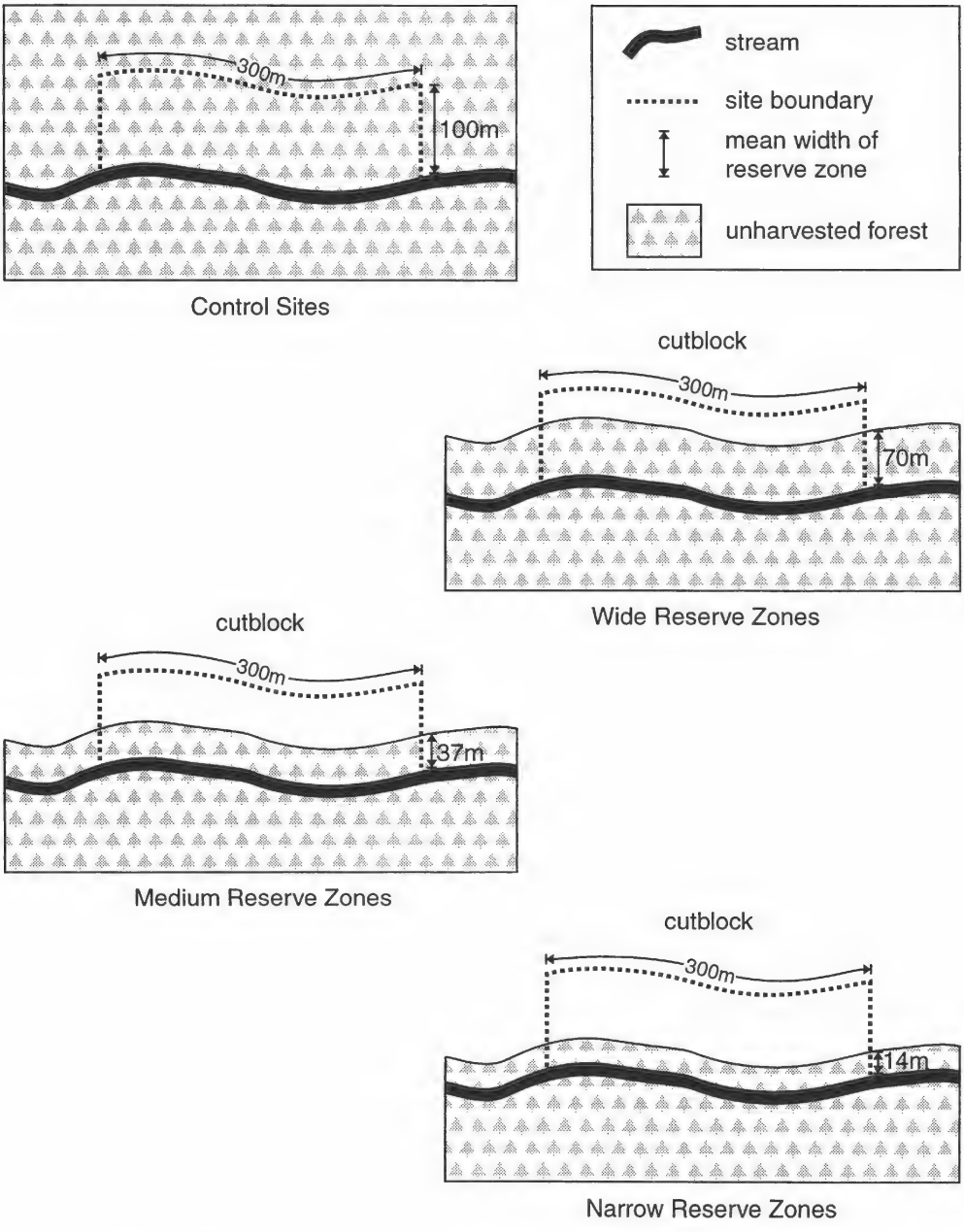

Figure 2. Control and treatment types.

them precluded the use of randomly-oriented transects, and made it necessary to sample from smaller plots (4 m radius) than recommended for forested habitats. For each habitat type at each site, four circular plots were drawn on habitat maps using random X and Y coordinates, then transferred to the field. Within each plot, the following data were recorded: number of snags, number of trees (>10 m tall), percent canopy cover (using a spherical densiometer), percent cover of the tall shrub stratum (2 to 10 m), and percent cover of the low shrub stratum (<2 m). Two-tailed t-tests were used to determine whether values differed among habitats. Because the study was intended to be exploratory rather than comprehensive, sample sizes were low and P values were not adjusted for multiple comparisons.

Each site was divided into a bird survey grid of twelve 50 m x 50 m plots, arranged in an array of six squares aligned parallel to the stream by two squares deep. The grid covered the entire 300 m x 100 m site. Thus, in all but controls it included both the cutblock and the reserve zone. Plot boundaries were marked on 1:1000 habitat maps. Each site was visited three times during May and June, once in each of early, mid and late morning. On each occasion, an observer spent five minutes at the center of each plot, marking locations on habitat maps of all birds seen or heard within the plot.

Species richness (number of bird species) was tallied for each site, and also for each habitat type in controls. Bird density (number of detections/ha) was calculated for each species and for all species combined. In control sites, density was calculated separately for riparian forest and upland forest. Riparian-associated species were defined by determining which species' populations were significantly more abundant in riparian forest than upland forest in control sites. This was accomplished using one-tailed t-tests for species which general references or other studies indicated were riparian-associated in similar ecosystems (Farrand 1983a, 1983b, 1983c, Godfrey 1986, Gyug 1995, Scott 1987, Campbell et al. 1990a, 1990b, Peterson 1990, Semenchuk 1992), and using two-tailed t-tests for other species. Densities of each riparian-associated species, all riparian-associated species combined, and all species combined were each compared (ANOVA) among treatments (narrow, medium or wide reserve zone). Controls were used to define riparian-associated species, as described above, but were not compared to reserve-zone treatments because bird use of streamside areas may be qualitatively different in reserve zones than in intact forest, as a result of temporary "packing" into reserve zones of birds that formerly occurred in adjacent logged land (Lehmkuhl et al. 1991, Gyug 1995). Thus, the presence of a bird in a reserve zone may not reflect the same level of use or habitat value that it would in a forest stand widely separated from cutting. A regression equation was calculated for reserve zone width (m) versus density of riparian-associated birds. Riparian-associated species were determined based on two years of data but other comparisons were based on one year, as the full range of treatments was only studied in one year. Species diversity and species equitability were also compared among habitat types for controls and among treatments using the following equations (Krebs 1989):

$$H = -\sum_{i=1}^{s} (p_i)(\log_{10} p_i)$$

where:

H = Shannon-Wiener index of species diversity

s = number of species at site

p_i = proportion of sample belonging to i^{th} species

$$J = H/\log_{10} S$$

where:

J = species equitability

S = number of species in all sites (as an approximation of the number in the community)

Results

In comparison to upland forest, riparian forest had greater canopy cover, a lower density of live trees, and greater tall shrub cover (Table 2). CWD volume, snag density and low shrub cover did not differ significantly between the two habitat types, although the calculated P value for CWD (0.19) suggests the possibility that CWD values were greater in riparian forest.

Within controls, species richness was similar between riparian forest and upland forest: mean richness per site was 7.3 for both riparian and upland, while total richness for all five sites was 22 for riparian and 19 for upland. Bird density was higher in riparian forest than in upland forest

TABLE 2. Riparian forest and upland forest habitat attributes in 15 mature stands of the Montane Spruce zone, Invermere Forest District, B.C., 1993-1994.

Habitat Attributes	Riparian Forest		Upland Forest		t-Test
	mean	SE	mean	SE	P
CWD (m^3/ha)	103	13	79	13	0.19
Canopy cover (%)	74	2	61	3	<0.01
Live trees (stems/ha)	666	56	82	85	0.04
Snags (stems/ha)	169	40	176	41	0.91
Tall shrubs (% cover)	15	2	10	1	0.05
Low shrubs (% cover)	23	3	21	2	0.59

for all species combined (12.2 versus 6.5 detections/ha, p=0.03) and for three individual species: golden-crowned kinglets (*Regulus satrapa*; 3.8 versus 2.3, p=0.04), Hammond's flycatcher (*Empidonax hammondii*; 1.7 versus 0.5, p=0.03) and winter wren (*Troglodytes troglodytes*; 0.5 versus 0.0, p=0.01). Species diversity and species equitability were also higher in the riparian (H_{RIP}=0.96, H_{UPL}=0.86; J_{RIP}=0.62, J_{UPL}=0.55). Species densities by habitat type are summarized in Table 3.

Riparian-associated birds were considered to be the three having greater densities in the riparian than upland, plus the Townsend's warbler (*Dendroica townsendi*)[1]. Densities of these four species combined differed between treatments (ANOVA, P<0.01; Table 4). This was also true for each of the riparian-associated species individually (P<0.01), except Hammond's flycatcher (P=0.26). The regression of reserve zone width versus density of riparian-associated birds (Figure 3) had a correlation coefficient (R^2) of 0.803 and the regression equation:

$$y = 0.093x - 0.303, \text{ where}$$

y = density of riparian-associated birds (detections/ha)

x = reserve zone width (m)

In addition, the density of all species combined differed significantly among treatments, with higher densities in wider sites (Table 4). However, species diversity and species equitability per site did not differ significantly between treatments (P=0.15), with mean values of H_{NAR}=0.84, H_{MED}=0.71, H_{WID}=0.89 and J_{NAR}=0.54, J_{MED}=0.46, J_{WID}=0.58. Densities by treatment for each species are summarized in Table 3.

Discussion

The differences between riparian forest and upland forest for several of the habitat attributes indicate that these forest types provided different environments. For example, riparian forest provided greater canopy cover with fewer trees, greater tall shrub cover and possibly more CWD than upland forest. These differences emphasize the importance of maintaining the riparian forest's structural attributes to provide landscape-scale habitat variability, particularly because species can be strongly associated with particular structural patterns (Marzluff and Lyon 1983, Sharpe 1996), and riparian forest composes a relatively small part of the landscape.

We found bird density, species diversity and species equitability to be higher and species richness to be similar in riparian forest compared to adjacent upland forest. This was true despite the riparian forest portion of control sites being considerably smaller than the upland portion (recall Table 1). These results suggest that, at least at the stand level, riparian areas have a disproportionately high value in maintaining diverse avifaunas in conifer-dominated forests of the Montane Spruce zone. Therefore, guidelines intended to maintain riparian forest are justifiable from an avian perspective. Our results are consistent with the findings of many other authors who reported greater abundance or diversity of birds in riparian areas compared to upland areas (Thomas et al. 1979a, Stauffer and Best 1980, Emmerich and Vohs 1982, Knopf 1985, Bunnell et al. 1991, Croonquist and Brooks 1993, Leung and Simpson 1994). However, the results of several studies indicated patterns opposite to this. McGarigal and McComb (1992) found that upland forest in the wet coastal region of Oregon had more diverse avifaunas and higher populations than adjacent riparian forest. The authors of the Oregon study suggested that their study area, relative to more arid regions, showed less contrast between riparian and upland habitats in terms of water availability, microclimate, and structural complexity. In fact, overstory cover, low shrub cover, snag density and conifer basal area were all greater in upland than riparian areas in their study. Habitat use by some individual species also differed greatly between our study and the Oregon study. We found golden-crowned kinglets and Hammond's flycatchers to be more abundant in riparian forest, and

TABLE 3. Mean density (detections/ha) of birds in 3-ha sites adjacent to streams in the Montane Spruce zone, Invermere Forest District, B.C. Comparisons of forest type are pooled for 1993 and 1994, and those of reserve zone width are from 1994.

Species	Forest Type					Reserve Zone Type						
	Riparian (n=5)		Upland (n=5)		t-Test	Wide (n=3)		Medium (n=5)		Narrow (n=2)		ANOVA
	mean	SE	mean	SE	P[a]	mean	SE	mean	SE	mean	SE	P
American Robin (*Turdus migratorius*)						0.04	0.04	0.03	0.03	0.00	0.00	0.78
Black-capped Chickadee (*Parus atricapillus*)	0.09	0.06	0.02	0.02	0.35	0.05	0.05	0.00	0.00	0.00	0.00	0.35
Brown Creeper (*Certhia americana*)	0.03	0.03	0.05	0.05	0.80							
Brown-headed Cowbird (*Molothrus ater*)						0.04	0.04	0.00	0.00	0.06	0.06	0.35
Calliope Hummingbird (*Stellula calliope*)	0.00	0.00	0.02	0.02	0.33							
Cedar Waxwing (*Bombycilia cedrorum*)	0.03	0.03	0.02	0.02	0.87	0.00	0.00	0.00	0.00	0.06	0.06	0.13
Chipping Sparrow (*Spizella passerina*)						0.09	0.09	0.09	0.09	0.06	0.06	0.96
Dark-eyed Junco (*Junco hyemalis*)	0.14	0.11	0.49	0.13	0.06	0.84	0.25	0.73	0.45	0.18	0.18	0.80
Golden-crowned Kinglet (*Regulus satrapa*)	3.76	0.66	2.31	0.35	*0.04	2.97	0.22	1.44	0.22	0.62	0.39	0.01
Gray Jay (*Perisoreus canadensis*)	0.15	0.15	0.00	0.00	0.33	0.18	0.04	0.00	0.00	0.00	0.00	0.01
Great Gray Owl (*Strix nebulosa*)	0.06	0.06	0.00	0.00	0.33							
Hairy Woodpecker (*Picoides villosus*)						0.04	0.04	0.00	0.00	0.00	0.00	0.35
Hammond's Flycatcher (*Empidonax hammondii*)	1.73	0.56	0.47	0.24	*0.03	2.02	0.71	1.19	0.30	0.62	0.51	0.26
MacGillivray's Warbler (*Oporonis tolmiei*)	0.06	0.06	0.00	0.00	0.33							
Mountain Chickadee (*Parus gambeli*)	0.00	0.00	0.02	0.02	0.33	0.00	0.00	0.00	0.00	0.06	0.06	0.13
Olive-sided Flycatcher (*Contopus borealis*)						0.09	0.09	0.00	0.00	0.00	0.00	0.35
Pileated Woodpecker (*Drycopus pileatus*)	0.04	0.04	0.00	0.00	0.33							
Pine Grosbeak (*Pinicola enucleator*)						0.04	0.04	0.00	0.00	0.00	0.00	0.35
Pine Siskin (*Carduelis pinus*)	0.59	0.38	0.68	0.27	0.84	1.08	0.76	0.54	0.20	0.76	0.38	0.67
Purple Finch (*Carpodacus purpureus*)						0.04	0.04	0.00	0.0	0.00	0.00	0.35
Red Crossbill (*Loxia curvirostra*)	0.91	0.91	0.62	0.50	0.78	2.30	2.17	0.09	0.09	0.06	0.06	0.34
Red-breasted Nuthatch (*Sitta canadensis*)	0.03	0.03	0.09	0.06	0.39	0.04	0.04	0.03	0.03	0.13	0.13	0.50
Red-naped Sapsucker (*Sphyrapicus nuchalis*)	0.54	0.54	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.17	0.17	0.13
Ruby-crowned Kinglet (*Regulus calendula*)	0.03	0.03	0.06	0.05	0.58	0.04	0.104	0.31	0.28	0106	0.06	0.70

continued, next page

TABLE 3, continued

Species	Forest Type: Riparian (n=5) mean	SE	Upland (n=5) mean	SE	t-Test P[a]	Reserve Zone Type: Wide (n=3) mean	SE	Medium (n=5) mean	SE	Narrow (n=2) mean	SE	ANOVA P
Rufous Hummingbird (*Selasphorus rufus*)	0.00	0.0	0.02	0.02	0.33	0.09	0.05	0.03	0.03	0.00	0.00	0.25
Solitary Vireo (*Vireo solitarius*)	0.00	0.00	0.15	0.09	0.12	0.44	0.37	0.00	0.00	0.00	0.00	0.24
Spruce Grouse (*Dendragapus candadensis*)	0.11	0.07	0.00	0.00	0.15							
Swainson's Thrush (*Catharus ustulatus*)	0.30	0.11	0.36	0.16	0.76	0.98	0.55	0.20	0.08	0.11	0.11	0.16
Townsend's Warbler (*Dendroica towsendii*)	1.26	0.47	0.67	0.33	*0.16	1.0	0.27	0.17	0.12	0.06	0.06	0.01
Varied Thrush (*Ixoreus naevius*)	0.20	0.12	0.05	0.05	*0.13	0.09	0.05	0.00	0.00	0.00	0.00	0.05
Warbling Vireo (*Vireo gilvus*)						0.23	0.22	0.00	0.00	0.00	0.00	0.07
Western Tanager (*Prinaga ludoviciana*)	0.00	0.00	0.08	0.08	0.33	0.25	0.25	0.00	0.00	0.00	0.00	0.35
White-winged Crossbill (*Loxia leucoptera*)	0.17	0.12	0.00	0.00	0.17							
Winter Wren (*Troglodytes troglodytes*)	0.49	0.17	0.00	0.00	*0.01	0.43	0.15	0.00	0.00	0.06	0.06	0.01
Yellow-rumped Warbler (*Dendroica coronata*)	0.25	0.13	0.30	0.11	0.79	0.21	0.11	0.48	0.35	0.24	0.01	0.79

[a] P values are based on one-tailed t-tests for species which other literature indicated were riparian-associated in similar ecosystems, and on two-tailed t-tests for other species (see methods). Species for which one-tailed tests were done are indicated with an *.

TABLE 4. Mean density (detections/ha*) of all bird species combined and of riparian-associated birds in ten 3-ha sites that included riparian reserve zones in the Montane Spruce zone, Invermere Forest District, B.C., 1994.

Species	Wide Res. Zone mean	SE	Medium Res. Zone mean	SE	Narrow Res. Zone mean	SE	ANOVA P
All species	13.7	0.9	5.3	0.7	4.3	0.1	<0.01
All riparian-associated spp.	6.5	0.7	2.8	0.3	1.4	1.0	<0.01
Golden-crowned Kinglet	3.0	0.2	1.4	0.2	0.6	0.4	<0.01
Hammond's Flycatcher	2.0	0.7	1.2	0.3	0.6	0.5	0.26
Townsend's Warbler	1.1	0.3	0.2	0.1	0.1	0.1	<0.01
Winter Wren	0.4	0.1	0.0	0.0	0.1	0.1	0.01

* based on total area in each site, which included riparian and upland forest plus cutblock

winter wrens to occur only in riparian forest, whereas in coastal Oregon, Hammond's flycatchers occurred only in upland sites, golden-crowned kinglets were more abundant in upland sites, and winter wrens were less abundant but present in upland sites. In Vermont, Spackman and Hughes (1994) found the greatest bird abundance on transects that were the greatest distance from the high water mark of streams (>150 m). Murray and Stauffer (1995) found in Virginia that some species were positively and some were negatively associated with the riparian, with no significant overall trends in relative abundance or species richness. The results of these latter three studies

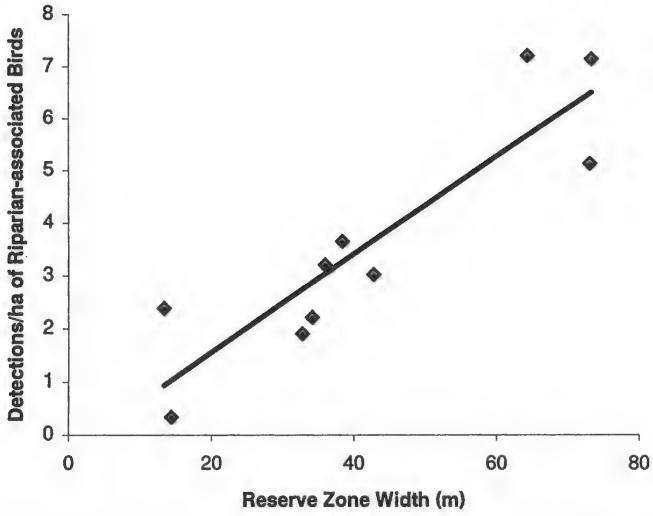

Figure 3. Density of riparian-associated birds in 10 100-m wide sites that included riparian reserve zones in the Montane Spruce zone, Invermere Forest District, B.C., 1994.

indicate that the value of riparian habitat to a given species, guild or community may differ widely between regions. Similarly, Knopf (1985) found that the relative significance of riparian areas varied along an elevational gradient. Our research and much of the literature generally support the theory that riparian areas are disproporionately important in maintaining diverse, abundant avifaunas, but their value cannot be generalized between regions or elevations. Management must therefore be based upon a local understanding of the distinctiveness of riparian habitat relative to upland habitat.

We found densities of riparian-associated birds and of all bird species combined to increase with width for riparian reserve zones averaging 14, 37 and 70 m. It is not known how far this trend would continue for even wider reserve zones. Controls were not compared to this trend because they had no definable width (there was no adjacent cutblock) and because habitat use by birds was probably qualitatively different in the contiguous forest of the controls, compared to the strips of forest and edge that made up the treatments. The observed pattern of increasing bird density with increasing reserve zone width occurred despite our census areas being the same width (100 m) for all reserve zone widths, the true riparian vegetation being intact in all sites, and the opposite bank providing a continuous block of intact forest. Given these facts, our results suggest that for narrower reserves 1) bird populations did not fully compensate for lost habitat by "packing" into a smaller forested area, as occurs in some fragmented forests (Lehmkuhl et al. 1991), or by making use of the adjacent cutblock, 2) riparian habitat value may be affected when adjacent upland forest is cut, even if the riparian itself is not cut, and 3) narrower riparian reserve zones are of less value than wider reserve zones, even if forest on the opposite side of the stream is intact. The low habitat value of narrow and medium reserve zones relative to wide reserve zones is consistent with most other studies. Three of the four species that we considered to be riparian associates and were sensitive to reserve zone width (Townsend's warbler, winter wren and golden-crowned kinglet) were also found to be sensitive to forested riparian corridor width by Gyug (1995) in habitats very similar to those we studied. Gyug found far fewer individuals of these species in reserve zones less than 50 m compared to those greater than 100 m, based on sites having reserve zones and cutblocks on both sides of the stream. In Quebec, Darveau et al. (1995) found that riparian reserve strips 60 m wide supported forest-dwelling birds in a pattern similar to controls, but that strips 20 or 40 m wide did not. In Iowa, Stauffer and Best (1980) found a positive correlation between reserve width and bird species richness for sites ranging from 10 to 250 m

wide. Croonquist and Brooks (1993) noted that sensitive species were absent from riparian reserves <25 m wide, and that reserves >125 m wide were needed to support a near-natural avifauna in Pennsylvania. Spackman and Hughes (1994) found that riparian corridors of about 175 m were needed to maintain 95% of the bird species found in control sites in Vermont. In contrast, Smith and Schaefer (1992) found very little difference in bird community characteristics between riparian reserves 20 to 60 m wide and those 75 to 150 m wide on urban streams in Florida, but felt this may have reflected an inadequate range of widths studied.

Differences in habitat characteristics and bird communities between riparian and upland forests support the practice of maintaining reserves in streamside forest. There are undoubtedly some species that are less abundant or less active in spruce-dominated riparian forest than in lodgepole pine-dominated upland forest. However, given the rarity of riparian forest relative to upland forest, differences in habitat attributes between riparian and upland, and the high species diversity and abundance in the riparian, it is prudent to preferentially provide protective management to riparian habitats in the Montane Spruce zone. Where partial cutting occurs in riparian forest, the differences in forest attributes that make riparian habitat unique from upland habitat should be maintained. Riparian wildlife might benefit if prescribed volumes of timber were removed in patches rather than uniformly, to ensure that at least part of the riparian habitat maintains its uniqueness and high habitat suitability. This hypothesis requires investigation, as it might also result in greater habitat fragmentation per volume of timber removed.

Depending on channel width, British Columbia guidelines require RMAs of 20 to 50 m on small streams, with only a portion of this being an RRZ and thereby being free from forest harvesting (BC Ministry of Forests and BC Environment 1995). Based on those guidelines, RMAs in the Montane Spruce zone may have considerably lower bird densities, including those of riparian associates, than they would if they were 70 m wide. A similar situation is likely to occur in Kootenai National Forest, where timber harvesting is restricted only in SMZs 30 m wide (Kootenai National Forest 1994). Furthermore, even the widest reserve zones studied, if isolated from contiguous mature forest, would probably be several orders of magnitude too small to maintain all species of neotropical migrants because of the small amount of habitat and expected high rates of nest predation and brood parasitism (Faaborg et al. 1993). Thus, if one goal of riparian management is to support near-natural densities of riparian-associated birds and maintain diverse avifaunas at the stand level, it appears that RMAs or SMZs should be wider than currently required under British Columbia or Kootenai National Forest guidelines, and should not be isolated from larger stands of mature forest.

Current riparian management guidelines in B.C. are not based on vegetational characteristics. A "riparian" management area will consist almost entirely of upland forest when the band of riparian vegetation is narrow, or alternatively, will maintain only a portion of the riparian forest when that vegetation type extends a great distance from the stream. This is likely because guidelines were developed to maintain recreational, aesthetic, fisheries and hydrological values, not just wildlife values. However, wildlife values and many other values could more adequately be maintained if prescribed widths of reserve zones, management zones and RMAs as a whole were seen as minimums, with provisions to enlarge them where riparian habitat extended greater distances from the stream, regardless of channel width, fisheries value, or use of a stream as a domestic water supply.

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Notes

1. The t-test for whether the Townsend's warbler occurs at greater density in the riparian than the upland yielded a P value of 0.16, which is generally beyond acceptable significance. However, a more extensive study in very similar habitat (Gyug 1995) found this species to be more common in the riparian (P=0.01), so it is included with other riparian associates in analyses of their response to treatments.

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Breeding Bird Abundance and Habitat Relationships on a Private Industrial Forest in the Western Washington Cascades

Abstract

Surveys were conducted to determine the presence, relative abundance, and habitat relationships of the breeding bird community on a private industrial forest (21,600 ha) in western Washington. A total of 284 and 299 point counts (8 min duration) were established in 1995 and 1996, respectively, along unpaved logging roads separated by a minimum distance of 240 m. The counts were performed twice, at least 10 days apart. A total of 9,491 detections of 78 species of breeding birds were detected at point count stations during the survey period with 40 species having >30 detections. A GIS analysis of forest habitat types was run for a 100-m radius circle centered on each survey point. Of 61 species tested by multiple regression analysis, significant positive regressions were revealed for the following habitat types: mature conifer habitat (>45 yr) for 32 species, pole-sized conifer habitat (27-44 yr) for 27 species, sapling-sized conifer habitat (6-26 yr) for 38 species, recent clearcut habitat (0-5 yr) for 32 species, non-forested habitat (including open water) for 20 species, and alder-hardwood habitat (all ages) for 19 species. Overall, the GIS-habitat/mutiple regression models demonstrated that all successional stages on an industrial forest were important to different groups of species within the breeding bird community. Species richness was equal or greater than observed in studies conducted on federal lands in the Pacific Northwest and suggested that industrial forests can be managed to make an important contribution to regional biodiversity of breeding birds.

Introduction

During the past 40 years, logging in Washington and Oregon has converted 80 to 90 percent of the original mature and old-growth forest into a complex mosaic of early and late-successional forest (Harris 1984, Meslow et al. 1981, Spies and Franklin 1988, Bolsinger and Waddell 1993). Previous breeding bird surveys in the southern Washington Cascades (Manuwal and Huff 1987, Manuwal 1991) and the central Oregon Coast Range (McGarigal and McComb 1992) were conducted on National Forest lands which generally receive different and less-intensive silvicultural treatments, but yet have a propensity for higher levels of forest fragmentation (Franklin and Foreman 1987, Li et al. 1993). Forest fragmentation is less of a concern for industrial forests because high harvest rates have resulted in nearly complete conversion of old forests into plantations (Spies and Franklin 1988) and the practice of clearcutting large blocks leaves few fragments (Lehmkuhl et al. 1991). Because of these fundamental differences in forest management, the characterization of breeding bird populations on private industrial forest land should be investigated to examine the potential of these lands to contribute to regional conservation and biodiversity efforts. Virtually all of the previous studies on breeding bird communities in the Pacific Northwest have been conducted on federal lands.

In this study, surveys were conducted to determine the presence, relative abundance, and habitat relationships of the breeding bird community on a private industrial forest in the western Washington Cascade range. The surveys were part of a monitoring plan which was required under a multi-species Habitat Conservation Plan (HCP) implemented by the landowner. However, the results of the study have valuable implications for monitoring populations and predicting habitat suitability on other northwestern industrial forests.

Study Area

The study area was the Mineral Tree Farm in Lewis County Washington, an industrial tree farm of about 21,600 ha in total area which is owned and operated by the Murray Pacific Corporation (Tacoma, WA). The tree farm is located along the western edge of the Southern Cascade Physiographic Province and ranges in elevation from about 300 to 1640 m. Approximately 19,600 ha of the tree farm are capable of supporting forest growth, with the remaining area containing rocky ridgetops, alpine meadows, cliff/talus slopes, roads, brush, standing water, and gravel pits. The timberlands fall within the *Tsuga heterophylla* Forest Zone (Franklin and Dyrness 1984), which is dominated by Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*). Western redcedar (*Thuja*

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plicata) is locally abundant, and Pacific silver fir (*Abies amabilis*) and noble fir (*A. procera*) are present at higher elevations. Commercial timber production is the dominant land use on the Mineral Tree Farm, which is characterized by stands of various age classes including recent clearcuts (0-5 yr; 12%), saplings (6-26 yr; 43%), pole forest (27-45 yr; 28%), and commercially mature forest (>45 yr; 15%). Isolated stands of old-growth forest (>250 yr) occurs on less than 2% of the tree farm. The area is characterized by a mild, wet maritime climate. Precipitation occurs mainly in winter and averages 180 to 360 cm annually.

Methods

We used the "extensive point count" technique to quantitatively sample the breeding bird community (Ralph et al. 1993). A total of 284 and 299 point counts were surveyed in 1995 and 1996, respectively, with 248 locations repeated in both years and a total of 330 different locations. Specifically, a fixed-distance point count was used, whereby all birds seen or heard during an 8-minute period were recorded (Manuwal and Huff 1987), if within 100 m of each observation point. Unlimited distance point counts are not recommended for most survey needs, especially where loud streams can reduce detection levels of birds (McGarigal and McComb 1992). All surveys were conducted by the author and two other qualified field biologists. During surveys, we also recorded aerial foragers that flew within 100 m above the ground (swifts, swallows, hawks, etc.) since they were probably using the point count habitat for foraging. Ralph et al. (1993) recommended that stations should only be sampled once a season for most breeding bird surveys, unless the goal is to get good estimates of small or rare habitats. We conducted two separate visits at each survey station to improve the probability of detection due to variables such as weather, nesting phenology, and time of migration. In 1995, the first visit was conducted from 15 May to 1 June. The second visit was conducted from 6 June to 29 June. In 1996, the first visit was conducted from 21 May to 31 May. The second visit was conducted from 3 June to 27 June. At least 10 days elapsed between visits during each year.

Surveys were usually conducted during fair weather, but occasionally were done during intermittent drizzle, misting, and light fog which did not decrease normal levels of bird activity and singing. Surveys were cancelled during significant rain, fog, or if winds exceeded 20 kmph. All surveys were conducted from sunrise to mid-morning hours, but did not go beyond 10:00 as recommended (Ralph et al. 1993). All field identifications, nomenclature, and taxonomy are consistent with Peterson (1990). A four-letter code (acronym) for each species was used in the field to record birds on original data forms as recommended by Ralph et al. (1993).

Point counts were established along driving routes to improve survey efficiency and were separated by a minimum distance of 240 m (0.15 mile) as recommended by Ralph et al. (1993) to avoid duplication of counting effort. The points were all located on unpaved logging roads (secondary and tertiary) as recommended by Ralph et al. (1993) and were marked with green vinyl streamers which indicated the site number for replicate visits to the site. The routes were systematically established throughout the tree farm in nearly all drainages and elevations containing driveable dirt roads.

A vector-based (ARC/INFO) Geographic Information System (GIS) was used to delineate six habitats as follows: commercially mature conifer (45+ years), pole conifer (27-44 years), sapling conifer (6-26 years), alder-hardwood (all ages), recent clearcut (0-5 years), and non-forested land (open water, rock, brush). Survey points were selected to provide an equivalent sample size from each forest habitat type as well as along wetlands, streams, and uplands. Each point was given a unique identification number and was plotted on 1:24,000 scale GIS color habitat maps of the Mineral Tree Farm.

After the surveys were completed, the data for each point count station were entered into a computer database spreadsheet (Lotus 1-2-3, Cambridge, Massachusetts). The data sets from the two years were combined and the total number of sites occupied by each species was calculated (% of 330 total stations occupied).

Due to previous timber harvesting patterns, relatively few points were placed in single forest habitat types, so sites were usually a composite of several different habitats. All point count locations from field maps were digitized into the GIS and habitat areas within a 100 m radius were calculated. A multiple regression analysis using ordinary least squares was used to determine relationships between breeding birds (dependent

variable) and corresponding habitat measures as independent variables. There are no underlying assumptions on the distribution of the independent variables in multiple regression analysis (Kerlinger and Pedhazur 1973), and therefore, data transformations were not applied to the GIS habitat data. In order to avoid problems with normality among the independent variables (bird counts), abundance values were converted to a non-parametric scale (presence =1, absence = 0) as used in logistic regression analysis (Robbins et al. 1989). This also eliminated common biases in abundance counts due to differences in species-specific breeding densities and territory sizes. A separate full-model (all variables included) multiple regression analysis was run for each species so that they would be directly comparable to each other and because stepwise procedures have recently been criticized for use in ecology by many investigators (see review by James and McCulloch 1990). All statistical analyses were run on a personal computer using version 5.03 of NCSS (Number Cruncher Statistical System, Kaysville, Utah). Results are presented only for breeding birds with at least one significant habitat regression ($p < 0.05$), but species habitat models with small sample sizes should be regarded with caution. One limitation of this model is that it may not completely compensate for species which nest and forage in different habitats (see Brown 1985 for examples), and therefore, the results reported herein should also be considered in light of the current knowledge of the nesting biology of the species.

Results

A total of 9,491 detections of breeding birds occurred during the two-year survey (Table 1). A total of 78 species of breeding birds were detected at point count stations over the two years. There were a total of 70 species observed in each year, although 16 species were only recorded in one of the two survey years. During the survey period, at least 40 species had >30 detections.

Survey Replication

Point counts were highly consistent between the two visits and between years for certain species (e.g., Hammond's flycatcher, Pacific slope flycatcher, winter wren, golden-crowned kinglet, varied thrush, song sparrow). For some permanent residents and early migrants, abundance was noticeably greater on the first visit, suggesting an earlier nesting phenology (e.g., blue grouse, northern flicker, black-throated gray warbler). Abundance was noticeably greater on the second visit for some species of late migrants (e.g., willow flycatcher, Swainson's thrush, warbling vireo, black-headed grosbeak). In both 1995 and 1996, 14 species were detected on only one of the two visits, thereby showing the value of replicating counts at least twice during the breeding season (at least 10 days apart).

Relative Abundance

Of 78 species detected on the survey, 10 were detected at more than 50 percent of the survey sites, including: Pacific slope flycatcher, winter wren, dark-eyed junco, American robin, Swainson's thrush, chestnut-backed chickadee, golden-crowned kinglet, Stellar's jay, varied thrush, and hermit warbler. Another 13 species were detected at between 20 and 50 percent of survey sites and six species were detected at 10 to 20 percent of survey sites. Three candidates for state-listing in Washington were also found during the survey, including: Vaux's swift (40 detections), pileated woodpecker (34), and western bluebird (3).

Habitat Relationships

A full-model multiple regression analysis was conducted with all six independent variables (GIS forest habitat types) for each breeding bird species. A total of 61 species had at least one 1 to 6 significant regressions with the six habitats used in the analysis (Table 2). For mature conifer habitat (>45 yr), significant positive regressions were revealed among 32 bird species. For pole-sized conifer habitat (27-44 yr), significant positive regressions were revealed among 27 bird species. For sapling-sized conifer habitat (6-26 yr), significant positive regressions were revealed among 38 species. For recent clearcut habitat (0-5 yr), significant positive regressions were revealed among 32 species. For non-forested habitat (including open water), significant positive regressions were revealed among 20 species. For alder-hardwood habitat (all ages), significant positive regressions were revealed among 19 species.

Discussion

This survey documented a diverse breeding bird community of 78 species occurring on the Mineral

TABLE 1. Breeding bird survey results from an industrial tree farm in the western Washington Cascades, Lewis County (284 point counts in 1995 and 299 point counts in 1996).

Species	Species Code	1995 Total Number Visit #1	1995 Total Number Visit #2	1996 Total Number Visit #1	1996 Total Number Visit #2	Total Number of Detections	Percent of Stations Occupied
mallard *Anas platyrhynchos*	MALL	4	1	0	8	13	0.6
common merganser *Mergus merganser*	COME	0	0	0	1	1	0.3
sharp-shinned hawk *Accipiter striatus*	SSHA	1	1	0	0	2	0.6
Cooper's hawk *Accipiter cooperii*	COHA	0	0	0	1	1	0.3
red-tailed hawk *Buteo jamaicensis*	RTHA	3	11	1	3	18	4.8
American kestrel *Falco sparverius*	AMKE	2	0	0	1	3	0.9
blue grouse *Dendragapus obscurus*	BLGR	36	18	41	29	124	24.9
ruffed grouse *Bonasa umbellus*	RUGR	13	3	1	0	17	4.8
band-tailed pigeon *Columba fasciata*	BTPI	8	4	10	4	26	5.1
common snipe *Gallinago gallinago*	COSN	0	0	3	1	4	0.6
great horned owl *Bubo virginianus*	GHOW	0	0	1	2	3	0.3
northern pygmy-owl *Glaucidium gnoma*	NPOW	2	1	0	1	4	1.2
common nighthawk *Chordeiles minor*	CONI	0	3	0	2	5	1.5
Vaux's swift *Chaetura vauxi*	VASW	11	0	25	4	40	3.6
rufous hummingbird *Selasphorus rufus*	RUHU	13	8	13	27	61	15.0
red-breasted sapsucker *Sphyrapicus ruber*	RBSA	10	5	4	7	26	5.7
red-naped sapsucker *Sphyrapicus nuchalis*	RNSA	0	2	0	0	2	0.6
downy woodpecker *Picoides pubescens*	DOWO	3	0	1	2	6	1.8
hairy woodpecker *Picoides villosus*	HAWO	36	35	51	23	145	29.6
northern flicker *Colaptes auratus*	NOFL	31	18	38	17	104	22.5
pileated woodpecker *Dryocopus pileatus*	PIWO	11	13	2	8	34	7.8
olive-sided flycatcher *Contopus borealis*	OSFL	15	22	20	16	73	14.4
western wood-pewee *Contopus sordidulus*	WWPE	1	0	1	2	4	1.2
willow flycatcher *Empidonax trailli*	WIFL	13	51	28	79	171	23.4
Hammond's flycatcher *Empidonax hammondii*	HAFL	23	22	16	24	85	13.8
Pacific slope flycatcher *Empidonax difficilis*	PSFL	241	249	212	271	973	83.8
tree swallow *Tachycineta bicolor*	TRSW	5	11	11	4	31	3.6
violet-green swallow *Tachycineta thalassina*	VGSW	4	6	1	4	15	2.1
no. rough-winged swallow *Stelgidpteryx serripennis*	NRSW	1	0	0	0	1	0.3
barn swallow *Hirundo rustica*	BASW	3	2	0	0	5	1.2
gray jay *Perisoreus canadensis*	GRJA	18	31	29	31	109	20.4
Steller's jay *Cyanocitta stelleri*	STJA	91	74	109	93	367	57.5
American crow *Corvus brachyrhynchos*	AMCR	4	2	2	2	10	0.9
common raven *Corvus corax*	CORA	4	4	11	11	30	5.7
black-capped chickadee *Parus atricapillus*	BCCH	1	0	5	0	6	0.9
chestnut-backed chickadee *Parus rufescens*	CBCH	79	67	146	133	425	61.4
red-breasted nuthatch *Sitta canadensis*	RBNU	48	33	42	34	157	31.1
brown creeper *Certhia americana*	BRCR	6	11	5	9	31	8.4
Bewick's wren *Thryomanes bewickii*	BEWR	1	0	0	0	1	0.3
house wren *Troglodytes aedon*	HOWR	2	1	0	1	4	1.2
winter wren *Troglodytes troglodytes*	WIWR	241	240	222	207	910	80.8
American dipper *Cinclus mexicanus*	AMDI	0	0	4	4	8	1.8
golden-crowned kinglet *Regulus satrapa*	GCKI	115	110	94	82	401	59.6
ruby-crowned kinglet *Regulus calendula*	RCKI	2	0	0	0	2	0.6
western bluebird *Sialia mexicana*	WEBL	2	1	0	0	3	0.3
Townsend's solitaire *Myadestes townsendi*	TOSO	17	6	9	16	48	9.9
Swainson's thrush *Catharus ustulatus*	SWTH	92	192	123	172	579	69.5
hermit thrush *Catharus guttatus*	HETH	15	17	45	42	119	20.4

continued, next page

Table 1, continued

Species	Species Code	1995 Total Number Visit #1	1995 Total Number Visit #2	1996 Total Number Visit #1	1996 Total Number Visit #2	Total Number of Detections	Percent of Stations Occupied
American robin *Turdus migratorius*	AMRO	89	66	74	100	329	55.7
varied thrush *Ixoreus naevius*	VATH	150	150	170	177	647	71.0
cedar waxwing *Bombycilla cedrorum*	CEWA	0	6	3	4	13	2.1
solitary vireo *Vireo solitarius*	SOVI	0	0	0	2	2	0.3
Hutton's vireo *Vireo huttoni*	HUVI	11	13	13	1	38	10.2
warbling vireo *Vireo gilvus*	WAVI	55	97	48	82	282	40.4
orange-crowned warbler *Vermivora celata*	OCWA	23	15	17	10	65	12.3
yellow warbler *Dendroica petechia*	YEWA	0	3	0	1	4	0.9
yellow-rumped warbler *Dendroica coronata*	YRWA	8	4	17	7	36	4.2
black-throated gray warbler *Dendroica nigrescens*	BGWA	67	33	45	39	184	27.2
Townsend's warbler *Dendroica townsendi*	TOWA	6	1	8	1	16	3.3
hermit warbler *Dendroica occidentalis*	HEWA	84	100	121	94	399	52.4
MacGillivray's warbler *Oporornis tolmiei*	MGWA	76	82	77	73	308	42.5
common yellowthroat *Geothlypis trichas*	COYE	0	1	0	0	1	0.3
Wilson's warbler *Wilsonia pusilla*	WIWA	87	73	72	66	298	47.0
western tananger *Piranga ludoviciana*	WETA	53	72	57	42	224	39.5
black-headed grosbeak *Pheucticus melanocephalus*	BHGR	14	28	22	29	93	18.9
rufous-sided towhee *Pipilo erythrophthalmus*	RSTO	21	20	26	24	91	17.7
fox sparrow *Passerella iliaca*	FOSP	0	0	1	0	1	0.3
song sparrow *Melospiza melodia*	SOSP	51	52	59	57	219	31.4
Lincoln's sparrow *Melospiza lincolnii*	LISP	6	1	3	0	10	1.5
white-crowned sparrow *Zonotrichia leucophrys*	WCSP	23	33	37	36	129	18.9
dark-eyed junco *Junco hyemalis*	DEJU	149	206	186	228	769	78.4
red-winged blackbird *Agelaius phoeniceus*	RWBL	3	8	4	1	16	1.5
brown-headed cowbird *Molothrus ater*	BHCO	1	0	1	0	2	0.6
red crossbill *Loxia curvirostra*	RECR	0	0	16	18	34	2.7
purple finch *Carpodacus purpureus*	PUFI	4	2	0	1	7	1.8
pine siskin *Carduelis pinus*	PISI	3	1	10	18	32	6.3
American goldfinch *Carduelis tristis*	AMGO	7	4	0	1	12	2.7
evening grosbeak *Coccothraustes vespertina*	EVGR	9	12	1	1	23	4.5
Totals		2228	2358	2414	2491	9491	

Tree Farm, with 40 species having >30 detections. Previous surveys in the southern Washington Cascades (Manuwal and Huff 1987) were on National Forest lands and detected only 46 species of breeding birds, even though young (42-75 yr), mature (105-165), and old-growth stands (250+ yr) were surveyed. That study used fewer point counts (42), but more replicates which may partially explain their lower total number of species. We also included wetlands and clearcuts in our sampling which undoubtedly helped to increase species richness for the tree farm. Surveys in Oregon (McGarigal and McComb 1992) found 55 breeding bird species at 96 point counts (only 10 species having >30 detections), but these surveys were limited to mature coniferous and hardwood forests. Surveys in Northern California/Southern Oregon (Ralph et al. 1991) found a similar number of species (71) in Douglas-fir/hardwood stands. Overall, the Mineral Tree Farm had a high species richness compared to previous Northwest investigations and contained virtually all of the breeding bird species expected for its geographic location.

The GIS-habitat/mutiple regression models demonstrated that all successional stages on an

TABLE 2. Results of multiple regression analysis of breeding bird occupancy versus GIS-habitat classes in a 100 m radius circle around point counts. Data listed under habitats are standardized beta coefficients (* indicates a probability < 0.05 that the slope of the regression is zero). R^2 is the overall adjusted r-squared value for the full-model multiple regression equation (P is the probability of the slope of the equation equalling zero).

Species Code	mature conifer >45 yr	pole conifer 27-44 yr	sapling conifer 6-26 yr	recent clearcut 0-5 yr	non-forested habitats	alder/ hardwoods	R^2	P
MALL	-0.031	-0.016	0.129*	-0.010	0.102	-0.022	0.018	0.092
RTHA	0.222*	0.018	-0.004	0.076	0.032	0.084	0.066	0.001
AMKE	-0.043	-0.018	0.064	0.167*	-0.001	-0.027	0.015	0.120
BLGR	0.276*	0.154*	0.137*	0.236*	0.027	0.043	0.254	0.001
RUGR	-0.021	0.226*	0.164*	0.020	-0.009	-0.009	0.072	0.001
BTPI	0.093	0.100	0.144*	0.086	-0.050	-0.030	0.046	0.002
VASW	0.111*	0.024	0.098	0.098	0.007	-0.038	0.031	0.018
NPOW	0.058	0.055	-0.026	0.038	-0.021	0.152*	0.021	0.062
RUHU	0.141*	0.098	0.197*	0.166*	0.059	0.020	0.142	0.001
RBSA	-0.030	0.096	0.246*	0.100	0.009	-0.052	0.075	0.001
DOWO	0.048	0.003	0.066	0.005	0.019	0.163*	0.026	0.031
HAWO	0.188*	0.096*	0.124*	0.414*	0.039	0.147*	0.359	0.001
NOFL	0.076	0.059	0.214*	0.380*	0.085	0.028	0.269	0.001
PIWO	0.184*	0.120*	0.022	0.146*	0.040	-0.017	0.083	0.001
OSFL	0.134*	0.001	0.249*	0.265*	0.028	-0.086	0.185	0.001
WIFL	0.056	0.048	0.267*	0.347*	0.078	0.073	0.272	0.001
HAFL	0.352*	-0.013	0.012	0.266*	0.017	0.005	0.237	0.001
PSFL	0.365*	0.412*	0.342*	0.294*	0.088*	0.179*	0.844	0.001
TRSW	-0.030	0.019	0.194*	0.045	0.135*	-0.026	0.059	0.001
VGSW	0.017	0.024	0.101	0.003	0.194*	-0.020	0.048	0.002
BASW	-0.012	0.095	-0.042	0.113*	0.129*	-0.033	0.023	0.049
GRJA	0.164*	0.247*	0.200*	0.134*	-0.016	0.070	0.204	0.001
STJA	0.217*	0.316*	0.400*	0.252*	0.068	0.091	0.571	0.001
AMCR	-0.042	-0.014	-0.005	-0.022	0.388*	0.058	0.142	0.001
CORA	0.110*	0.136*	0.098	0.053	-0.011	0.039	0.048	0.002
BCCH	-0.035	0.028	-0.024	0.047	0.186*	0.097	0.035	0.010
CBCH	0.373*	0.337*	0.314*	0.190*	0.104*	0.110*	0.626	0.001
RBNU	0.418*	0.128*	0.107*	0.254*	0.018	0.063	0.376	0.001
BRCR	0.314*	0.098	-0.013	0.071	0.061	0.007	0.125	0.001
HOWR	0.024	-0.022	-0.026	0.081	0.045	0.178*	0.032	0.015
WIWR	0.356*	0.435*	0.351*	0.252*	0.071*	0.177*	0.818	0.001
AMDI	0.075	0.121*	-0.034	0.032	0.004	0.087	0.019	0.076
GCKI	0.448*	0.418*	0.294*	0.102*	0.005	0.102*	0.657	0.001
TOSO	0.232*	0.053	0.032	0.253*	-0.022	-0.035	0.144	0.001
SWTH	0.276*	0.304*	0.431*	0.253*	0.116*	0.125*	0.695	0.001
HETH	0.200*	0.136*	0.297*	0.098	0.082	-0.080	0.220	0.001
AMRO	0.240*	0.222*	0.262*	0.377*	0.167*	0.132*	0.577	0.001
VATH	0.347*	0.389*	0.402*	0.184*	0.078*	0.101*	0.718	0.001
CEWA	0.087	-0.026	0.116*	0.017	0.029	0.039	0.018	0.088
HUVI	0.066	0.232*	0.145*	0.099	-0.039	0.061	0.108	0.001
WAVI	0.039	0.141*	0.397*	0.264*	0.146*	0.221*	0.465	0.001
OCWA	-0.001	0.074	0.370*	0.107*	0.067	-0.043	0.175	0.001
YRWA	0.106	-0.002	0.176*	0.055	0.032	-0.043	0.047	0.002
BGWA	0.150*	0.405*	0.144*	0.065	0.028	0.257*	0.358	0.001
TOWA	0.134*	0.229*	0.032	-0.030	-0.028	-0.027	0.060	0.001
HEWA	0.416*	0.378*	0.196*	0.182*	0.076*	0.057	0.561	0.001
MGWA	0.112*	0.034	0.417*	0.398*	0.100*	0.091*	0.504	0.001
WIWA	0.146*	0.268*	0.431*	0.186*	0.098*	0.099*	0.487	0.001

continued, next page

TABLE 2, continued

Species Code	mature conifer >45 yr	pole conifer 27-44 yr	sapling conifer 6-26 yr	recent clearcut 0-5 yr	non-forested habitats	alder/ hardwoods	R^2	P
WETA	0.361*	0.145*	0.193*	0.294*	-0.044	0.177*	0.448	0.001
BHGR	0.019	0.139*	0.166*	0.298*	0.084	0.127*	0.213	0.001
RSTO	0.061	0.026	0.203*	0.318*	0.065	0.092	0.209	0.001
SOSP	0.042	0.012	0.339*	0.389*	0.187*	0.059	0.410	0.001
LISP	-0.020	-0.004	0.016	0.039	0.376*	-0.048	0.132	0.001
WCSP	0.089	0.021	0.134*	0.425*	0.079	0.025	0.261	0.001
DEJU	0.237*	0.328*	0.388*	0.424*	0.120*	0.102*	0.795	0.001
RWBL	-0.044	0.042	0.145*	0.008	0.115*	-0.032	0.030	0.019
RECR	0.132*	0.022	0.063	0.065	0.020	-0.034	0.022	0.052
PUFI	-0.048	-0.026	0.088	0.022	0.244*	0.080	0.077	0.001
PISI	0.223*	0.049	0.105	0.098	-0.055	-0.045	0.080	0.001
AMGO	0.000	0.085	-0.024	0.056	0.051	0.274*	0.085	0.001
EVGR	0.154*	0.148*	0.006	0.073	0.041	-0.042	0.051	0.001

industrial forest were important to different groups of species within the breeding bird community. Among the species that tended to be specialists (only 1 to 3 significant regressions), there were four distinct patterns that separated them from generalist species. Late successional species had their greatest affinity with mature conifer habitat (Fig. 1a). This group included two snag-dependent species: Vaux's swift and brown creeper, which require snags for nesting, roosting, or foraging (Brown 1985), as well as conifer seed-eaters that need to forage among mature mast-producing conifers (pine siskin, evening grosbeak, and red crossbill), and a large raptor which requires tall canopy trees for nest placement (red-tailed hawk).

Mature forest/edge species (Fig. 1b) differed from late-successional species by virtue of the inclusion of clearcut habitat with mature conifer habitat. This group included two snag-dependent species which typically inhabit late-successional forest: pileated woodpecker and red-breasted nuthatch (Brown 1985; Bull et al. 1986). The association of pileated woodpecker and red-breasted nuthatch with mature conifer forest and clearcuts was not due to a correlation between these two habitats (r = -0.12). Instead, it is possible that they were attracted to clearcut edges because of the higher levels of blowdowns, damaged trees, and mortality that can occur here (Norse 1990), as well as by snags, residual trees, logging slash, and stumps which were left behind in recent clearcuts. Bull et al. (1986) found that pileated woodpeckers foraged 36% of the time on downed logs and 29% in snags. Bull and Meslow (1977) also determined that 14% of feeding sites on dead wood were on stumps. In addition, Smith (1986) noted that damaged trees can produce large "distress crops" of seeds, and therefore, red-breasted nuthatches may also be attracted by local cone crop abundance along recent clearcut edges. Also in this group were three perch-hunting insectivores: olive-sided flycatcher, Hammond's flycatcher, and Townsend's solitaire, which are known to prefer forest-edge habitat (Brown 1985; Sharp 1992).

Early successional species (Fig. 1c) showed a decreasing trend of association with the successional stages, with the greatest affinity for clearcut and sapling habitats. This group included several ground foragers (white-crowned sparrow, song sparrow, and rufous-sided towhee), four shrub/sapling foragers (willow flycatcher, black-headed grosbeak, orange-crowned warbler, yellow-rumped warbler), and one open-terrain raptor (American kestrel).

As would be expected, the GIS-habitat models for alder/hardwood species (Fig. 1d) showed little association with conifer habitats, regardless of successional stage. This group included four cavity-nesters (downy woodpecker, house wren, northern pygmy-owl, and black-capped chickadee) with well-known affinities for deciduous or mixed conifer-hardwood stands (Brown 1985; Sharp 1992). American goldfinch is a seed-eater known to inhabit alder or other hardwood types

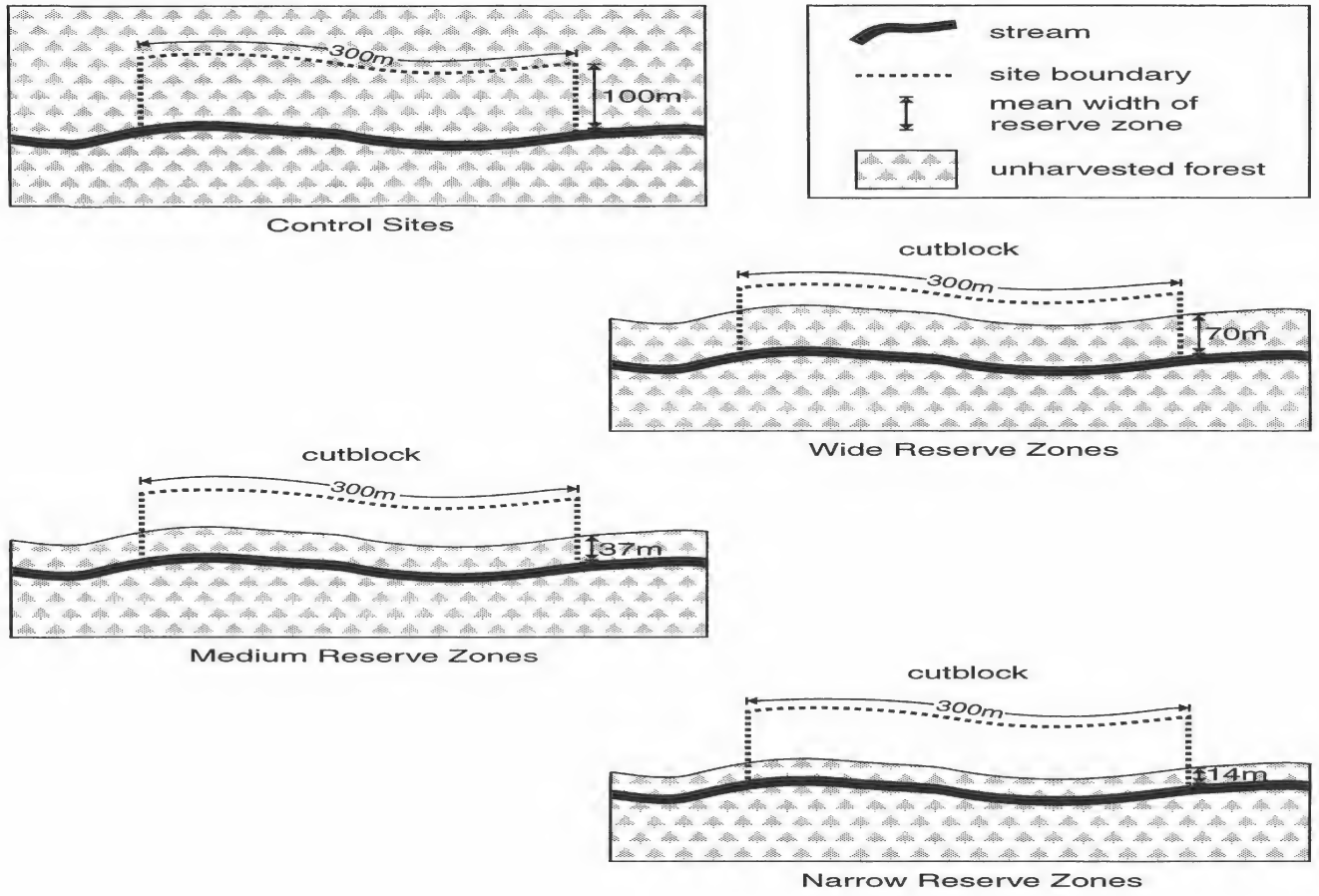

Figure 1. Groups of breeding bird species with similar habitat correlations from the GIS-habitat/multiple regression model (data represent standardized beta coefficients from Table 2). Species codes are given in Table 1.

(Brown 1985). None of these species were abundant because of the dominance of conifers on the Mineral Tree Farm.

Most of the 32 species that were significantly correlated with mature conifer in the GIS-habitat models were also observed to attain high abundance levels in mature and old-growth stands in other Northwest studies (Manuwal and Huff 1987, Manuwal 1991, Ralph et al. 1991). These strong similarities validate the utility of the GIS-habitat/multiple regression model which was developed for this study, as well as emphasize the value of maintaining mature forest habitat on private industrial forests for breeding birds. On the Mineral Tree Farm, mature conifer stands (>45 yrs) usually had higher densities of snags and remnant old-growth trees ("old-growth legacies"), than pole stands because of "sloppy clearcutting" and "high-grading" practices which were the norm before 1930 (McKelvey and Johnston 1992). Since that time, a chronic shortage of snags and large residual trees has occurred in clearcut units with the advent of "modern" intensive silviculture (Neitro et al. 1985). Intensive site preparation, concerns for worker safety, and salvage for wood chips and firewood have all contributed to a shortage of cull trees, snags, and residual trees in the Pacific Northwest (Neitro et al. 1985).

To mitigate for this predicted loss to wildlife diversity, special forest management prescriptions for the Mineral Tree Farm were developed in their HCP. These prescriptions require 30 m no-harvest buffers for wetlands and fish-bearing streams, 15 m buffers along approximately 59% of non-fish-bearing streams, and large quotas for snag/green-tree retention (i.e., 10 snags and 10 green trees must be left per ha of clearcut). No-harvest riparian buffer zones have been shown to retain most of the breeding bird species two years after clearcutting an area (Triquet et al. 1990). In addition, higher snag densities on clearcuts have been shown to produce a higher density and species richness of cavity-nesting birds (Schreiber and deCalesta 1992). The preferred use of uplands by many forest breeding birds in Oregon (McGarigal and McComb 1992) suggests that it is also important to maintain residual trees (seed trees, culls, and leave trees), snags, and no-harvest reserve areas in upland areas as well. If properly managed, industrial forests can make an important contribution to regional biodiversity and conservation of breeding birds.

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Northern Flying Squirrel Seasonal Food Habits in the Interior Conifer Forests of Central Idaho, USA

Abstract

Microhistological analysis of 200 scats collected from two artificial nest boxes used by northern flying squirrels (*Glaucomys sabrinus*) in central Idaho show distinct seasonal variation. The flying squirrels consumed hypogeous, mycorrhizal fungi in the summer and arboreal lichens and hypogeous, mycorrhizal fungi in the winter. Dominant summer foods included boletoid genera and *Leucogaster*, while dominant winter foods include lichens in the genus *Bryoria*, boletoid genera and the genus *Gautieria*. Central Idaho conifer forests developed under a continental climate characterized by summer drought and long, snow-covered winter and spring conditions. These climatic and vegetation conditions are considerably different from those found west of the Cascades where most studies of northern flying squirrels have been conducted.

Introduction

Studies of northern flying squirrel (*Glaucomys sabrinus*) diets in western North America (McKeever 1960, Fogel and Trappe 1978, Maser et al. 1978, Maser et al. 1985, Carey 1991, Hall 1991, Carey 1995) suggest a complex functional relationship in which mycorrhizal fungi critical to the growth of trees are dispersed by arboreal rodents. West of the Cascade Mountains, the diet of the northern flying squirrel consists largely of fungi. East of the Cascade Mountains and in Alaska, where winters are long and snow-covered, northern flying squirrels consume fungi and arboreal lichens (Maser et al. 1986, McKeever 1960, Mowrey et al. 1984). Lichen species reported in flying squirrel diets include: *Bryoria fremontii* (Tuck.) Brodo and Hawksworth (Maser et al. 1986), *Alectoria fremontii* (*Alectoria* syn.= *Bryoria)* and *Usnea ceratina* Ach. (McKeever 1960), *Usnea barbata* (L.) Weber ex Wigg. (Cowan 1936), and *Letharia, Physcia,* and unidentified lichens (Hall 1991). Other authors have merely classified the observed food by the category "lichens" (Conner 1960, Maser et al. 1978).

Unfortunately voucher specimens of lichens were either not made or have not been located for studies by Maser et al. (1986), McKeever (1960), or Mowrey and Zasada (1984), leaving the taxonomy unverified. The complexity of lichen taxonomy, which in some cases requires chemical tests for species determinations, raises doubts regarding the identity of some lichen genera and species reported. An understanding of the taxa consumed by flying squirrels is further confused because the genus *Usnea* has frequently been misapplied to *Alectoria,* which it superficially resembles both morphologically and ecologically. *Alectoria* has been subdivided (Brodo and Hawksworth 1977) into several genera, including *Alectoria* and *Bryoria*. We suspect that many reports of *Usnea* are either *Alectoria sarmentosa* or *Bryoria* species.

Therefore, based on chemistry and taxonomic confusion, we suggest that flying squirrels do not regularly consume any of the previously reported lichen taxa except *Bryoria fremontii,* which lacks secondary chemical compounds (Brodo and Hawksworth 1977, Rosentreter and Eslick 1993).

Previous studies have identified lichen fragments from stomach contents or scats of the northern flying squirrel. In studies of northern flying squirrel recovery in West Virginia, Mitchell (1994) recorded lichen presence in scats by quantifying the presence of algal cells.

In this study, we sought to identify the range of foods consumed by northern flying squirrels in an interior forest of the Northern Rocky Mountains. We were particularly interested in the diversity of mycorrhizal fungi eaten by the squirrels and the relative consumption of fungi and

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lichen. We also wished to determine the seasonal variation in foods consumed in light of the long period of deep snow-cover experienced by squirrels in this region.

Study Area

We examined flying squirrel scats collected on the Payette National Forest in central Idaho near McCall, Idaho, USA. Scats were collected in two drainages, the North Fork Payette River and Goose Creek. The Payette National Forest is mountainous; elevations range from 1,520 to 2,140 m. Its climate has a strong Pacific coastal influence during winter but follows continental patterns in summer (Finklin 1988). Annual precipitation averages over 100 cm a year and falls largely as snow, which accumulates to depths of 1.5 to 2 m. In most years 50% of the ground at higher elevations is covered by snow until after June 1st. The landscape is dominated by conifer forests, most stands supporting a sparse shrub layer but an extensive ground layer of low shrubs (*Vaccinium*), grasses, and forbs. Forest types included spruce-fir (*Picea engelmannii* Parry- *Abies lasiocarpa* (Hook.) Nutt.), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and lodgepole pine (*Pinus contorta* Dougl.) (Steele et al. 1981).

Methods

Field Methods

Northern flying squirrel scats were collected in 1989 from a system of artificial wooden nest boxes established on the Payette National Forest (Hayward and Rosentreter 1994). Scats deposited during the winter months and collected in early June when snow still covered the ground were classified as winter scats. Scats deposited from June through August were classified as summer scats. These seasonally produced scats differed in color and hardness; winter scats were harder and darker.

Some boxes were used as communal latrines rather than roosts or natal nests and provided a large number of scats, numbering from 20 to 400 per box. Two such latrine boxes from comparable habitats were sampled and analyzed. One latrine box contained summer scats and the other contained only winter scats. Both latrine box sites were in older aged stands (greater than 180 years old) with north-facing aspects classified as potential *Abies lasiocarpa* habitat series (Steele et al. 1981) at ca. 1920 m elevation. The winter scat box site was dominated by *Abies lasiocarpa* while the summer scat box was dominated by *Pinus contorta.* The two communal latrine boxes probably represent scats from between 2-12 individual squirrels. Maser et al. (1981) reported aggregations of northern flying squirrels, and we have observed up to six adult squirrels in a nest box at one time. Scats were stored dry until analysis began in December 1993.

Laboratory analysis

Dried flying squirrel scats were placed in formalin (4% formaldehyde) to prevent any exposure to Hantavirus. One hundred scats were randomly selected from each of the two large communal latrines. Each scat was soaked in a glass vial in approximately 2 ml formalin and then set on a slide warmer at 45°C for 24 hours (summer scats) or 48 hours (winter scats) to soften. Winter scats were harder and required more time to soften. After the warm soaking, scats were crushed in the glass vials with a glass rod. An eyedropper was inserted into the vial and squeezed quickly eight times to thoroughly mix the sample. One drop of the mixture was placed on a clean glass slide. Two drops of Melzer's solution were added. The slide was allowed to partially air dry. Two drops of Poly-vinyl alcohol (PVA) were then added, and a plastic cover slip was placed over the material. Ten random area views were examined under a light microscope at 400x, or when viewing larger structures, 100x. This method was a modification of Colgan et al. (in press), Maser et al. (1986) and McIntire and Carey (1989). Algal cells were compared to fresh specimens of the common *Bryoria* species from the study area (Hayward and Rosentreter 1994). All *Bryoria* species contained the algal genus *Trebouxia*. *Trebouxia* are green, single-celled algae with round to ovate cells and a distinctive starch pyrenoid. Nomenclature for the lichens follows Egan (1987). Fungal spores were identified by use of Castellano et al. (1989). Nomenclature for fungi follows that used by Castellano et al. (1989).

Permanent voucher slides were made of each type of fungal spore by adding five or more drops of PVA and drying slides on a warmer at 30°C for approximately 30 minutes. Voucher specimens of spores were verified by Teresa Label, Wesley Colgan III, and Michael Castellano.

Voucher slides are stored with the mycological collections at the Snake River Plains Herbarium (SRP) at Boise State University.

The presence of each type of fungal spore, vascular plant tissue, or algal cell was recorded and frequency of occurrence calculated for each type of material (Holechek and Gross 1982). Abundance, relative density, or percentage by volume (Maser et al. 1978) were not rated due to different spore sizes, making these ratings difficult and inaccurate (Williams 1987).

Results

Seasonal Variation

Results from microhistological investigations demonstrated distinct differences between summer and winter scats (Fig. 1). Dominant summer foods included boletoid genera and *Leucogaster*, while dominant winter foods were *Bryoria* lichens, boletoid genera and the genus *Gautieria* (Fig. 1). The greater dependence on lichens in the winter is indicated by the higher frequency of algal cells in the scats.

Lichens

Winter scats contained a higher frequency of *Trebouxia* (86%), the phycobiont alga for the arboreal lichen *Bryoria*, than the summer scats (25%) (Table 1). The winter scats also had a higher incidence of intact lichens, suggesting that as fungi became scarce in winter, lichens were more frequently eaten.

Fungi

Flying squirrel scats contained spores representing many taxa of fungi (Table 1). The Ascomyotina fungi that are lichenized are considered lichen and are not included here as Ascomyotina. The percentage of Ascomycotina to Basidiomycotina consumed was 36/64% in the winter and 27/73% in the summer (Table 1). All these fungi are predominantly hypogeous, with most forming ectomycorrhizal associations with tree roots. The

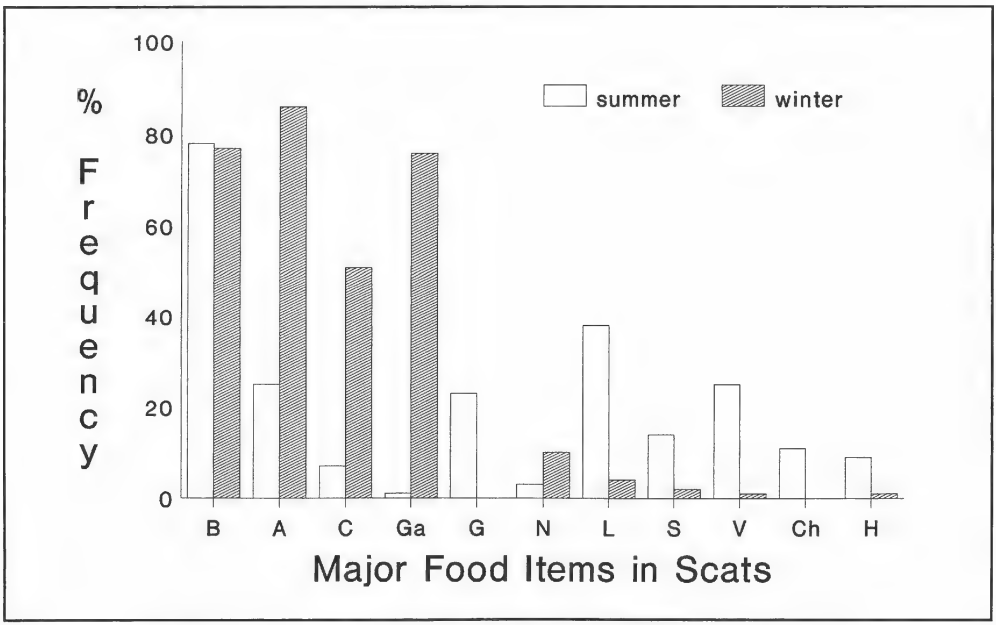

Figure 1. Major winter and summer food items in scats of northern flying squirrels. Scats collected from two nest boxes (2,000 views of 200 scats; 100 scats each from summer and winter periods). Symbols used for the major food items in order that they appear: B=Boletoid genera, A=Algae indicating lichens, C=Cortinarioid genera, Ga=Gautieria, G=Genea, N=Nivatogastrium, L=Leucogaster, S=Sclerogaster, V=Vascular plant tissue, Ch=Choiromyces, H=Hydnotrya.

TABLE 1. Percent frequency of occurrence in winter and summer foods of northern flying squirrels from 2,000 views of 200 scats (100 scats each from summer and winter periods). Trace amounts (t) were less than 1%.

Genus or Type of Material	Percent Frequency of Occurrence	
	Winter	Summer
Lichen, algae	86	25
Fungi		
Ascomycotina		
Pezizales		
Choiromyces	11	
Fisherula	t	1
Genea	t	23
Geopora	8	t
Hydnotrya	1	9
Pachyphloeus	t	t
Peziza	4	8
Picoa	t	-
Sarcosphaera	t	-
Tuber	t	2
Elaphomycetales		
Elaphomyces	2	t
Gautieriales		
Gautieria	76	1
Basidiomycotina		
Agaricales		
Cortinarioid genera	63	7
Russuloid genera	3	3
Boletales		
Boletoid genera	77	78
Hymenogastrales		
Octarianina	t	4
Sclerogaster	2	14
Lycoperdales		
Radiigera	1	1
Melanogastrales		
Leucogaster	4	38
Melanogaster	1	2
Phallales		
Hysterangium	t	t
Podaxales		
Endoptychum	t	-
Nivatogastrium	10	3
Zygomycotina		
Endogonales		
Glomus	t	-
Modicella	t	-
Sclerocystis	t	-
Vascular plant tissue	1	25

sporocarps of hypogeous fungi vary from 0.3- 5+ cm in size. Many fruit near the soil surface or beneath the litter layer while others are produced within the soil, where they are protected by the litter layer, and can persist for several weeks (Maser et al. 1978). The genera of hypogeous fungi consumed represent diverse species and ecological niches. *Alpova, Gastroboletus, Rhizopogon, Truncocolumella*, and *Trappea* were grouped as "boletoid genera" due to similar spore morphology and size. *Cortinarius* and *Hymenogaster* were grouped as "cortinarioid genera" due to similar spore morphology. Epigeous fungi such as *Peziza* was consumed in small amounts and only in the summer (Table 1). The genera of fungi consumed in winter differed greatly from those consumed in summer (Fig. 1). Northern Flying squirrel summer diets contained a wider range of genera, while the winter diet relied heavily on four to five genera.

Discussion

Flying squirrel diets were more varied in summer than winter, largely as a consequence of a greater array of fungi being consumed. This increased variety in the summer diet is similar to the trend observed by Carey (1995) west of the Cascade Mountains. Boletoid genera were frequent in both summer and winter diets in Idaho. The boletoid genera are a large group of common, small-spored mycorrhizal, hypogeous fungi that can be stored for winter food or harvested around the tree wells upon snow melt.

The most significant seasonal change in the fungal diet of the northern flying squirrel in Idaho was the increase from 1% to 76% frequency of *Gautieria* from summer to winter (Fig. 1, Table 1). *Gautieria* is very odoriferous and dries more readily than the other fungi (Trappe, personal communication). Observations in the Cascades indicate *Gautieria* is often found cached in trees during the summer months (Trappe, personal communication). The high incidence of *Gautieria* in the winter diet in Idaho suggests that squirrels may frequently cache these sporocarps for winter consumption or find dried sporocarps in patchy, snow-free areas. The most common *Gautieria* species in the study area is *G. monticola*.

In our study, the winter diet contained a higher frequency of "cortinarioid genera" than in other studies. In general, winter scats were harder, more dense, and contained fewer vascular plant tissue fragments and more whole lichen fragments than the summer scats. These dietary results are more

detailed but similar to those found in eastern Oregon by Maser et al. (1986).

Forest Management Implications

Mycorrhizal fungal diversity and forest health are directly linked (Maser et al. 1985). Thus, forest managers concerned about forest health should strive to maintain healthy mycorrhizal fungi populations, particularly critical in the dry interior forests. The role of flying squirrels in forest ecosystem functions, specifically as fungus and lichen dispersers, may be more critical in these interior forests than in the more diverse coastal forests (Trappe, personal communication). Maintaining flying squirrels may facilitate fungal diversity. Forest managers must recognize the importance of lichens, fungi, and tree cavities for the maintenance of northern flying squirrel populations and ultimately forest productivity.

Conclusions

Seasonal weather patterns in the conifer forests of the northern Rockies demand shifts in the food habitats of many animals, including the northern flying squirrel. In central Idaho, the dominant summer foods included boletoid genera and *Leucogaster*, while dominant winter foods were *Bryoria* lichens, boletoid genera and the genus *Gautieria*. Based on the abundance of *Gautieria* spores in winter scats and the deep snow of winter, we suggest that *Gautieria* is cached during the summer and consumed in the winter.

Flying squirrels may play an important role in ecosystem function through the dispersal of mycorrhizal fungi. Trees require these mycorrhizal fungi for growth and without dispersal and the resulting species mixing, the fungal diversity in the forest may decrease. Therefore, the interdependence and functional relationships among mycorrhizal fungi, conifers, flying squirrels, and arboreal lichens suggests a coevolution requiring each component for the optimal functioning of the interior coniferous forest.

We believe that lichens may also be seasonally utilized by northern flying squirrels in other regions, but researchers are either unaccustomed to analyzing scats for lichens, or the squirrels remain unstudied due to snow cover in the winter months. The long period of snow cover and deep snow depths found in the northern Rockies, however, may lead squirrels to depend on lichen to a greater extent in this climate. Because winter constitutes the major stress period for these and other arboreal rodents, research should begin to include or focus on this critical season.

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Food Preferences of Captive Northern Flying Squirrels from the Lassen National Forest in Northeastern California

Abstract

Hypogeous sporocarps of mycorrhizal fungi (truffles) are a common food of northern flying squirrels (*Glaucomys sabrinus*) and many other species of small mammals. Forest management practices and natural disturbances can affect both total amounts and species composition of truffles. We conducted cafeteria-style feeding trials to compare preferences of northern flying squirrels captured in the Lassen National Forest in northeastern California among sporocarps of 5 species of fungi (3 truffle species and 2 species of secotioid fungi), 2 species of lichens, and fir (*Abies magnifica* and *A. concolor*) seeds. Feeding trials were performed on 7 male squirrels for 4 consecutive nights. Mean proportion of food eaten varied significantly among the 3 truffle species, between the 2 species of secotioid fungi, and between the 2 lichen species. Mean proportion of food eaten was greatest for 2 of the truffle species, followed by the lichen *Bryoria fremontii*. These results indicate that northern flying squirrels preferred truffles over certain types of other naturally occurring foods, and that preference varied significantly among sporocarps of different fungal species. Natural disturbance and forest management that alter the species composition of fungal sporocarps are likely to affect the availability of foods preferred by northern flying squirrels.

Introduction

Numerous species of small mammals feed on hypogeous sporocarps of mycorrhizal fungi (hereafter referred to as "truffles") in temperate and tropical forests throughout the world (e.g., Tevis 1953, Fogel and Trappe 1978, Maser et al. 1978, Taylor 1992, Johnson 1994, Janos et al. 1995). Some species, such as the northern flying squirrel (*Glaucomys sabrinus*), California red-backed vole (*Clethrionomys californicus*) (Ure and Maser 1982), and various species within the marsupial family Potoridae (Taylor 1992, Claridge and Cork 1994, Johnson 1994) are highly mycophagous and feed on truffles as one of their primary food sources. Although sporocarps are consumed, spores are viable after passage through small mammal digestive tracts (Trappe and Maser 1977, Cork and Kenagy 1989, Claridge et al. 1992), and Cork and Kenagy (1989) showed that passage through the digestive tract of a species of ground squirrel enhanced spore germination. Because most species of fungi that produce hypogeous sporocarps eaten by small mammals are thought to be mycorrhizal, mycophagous small mammals contribute to the maintenance of mycorrhizal symbioses (Trappe and Maser 1977, Maser et al. 1978).

In a previous study we evaluated associations between northern flying squirrel density and forest structure in fir (*Abies* spp.) stands in the Lassen National Forest in northeastern California (Waters and Zabel 1995). We found truffles in each of the 155 flying squirrel fecal samples examined, and flying squirrel density was correlated with frequency of hypogeous sporocarps across the 12 stands in which we sampled. Lichens, unknown vegetative matter, spores from epigeous fungi, pollen from conifer staminate cones, insect parts, and seed parts were also observed in fecal samples. In another study, we found significant association between thinning level (heavily thinned, moderately thinned, and unthinned) and frequencies of the 5 most common truffle genera, suggesting that thinning led to changes in the composition of truffle species (Waters et al. 1994). We also found significant association between stand age (old-growth and mature stands that originated after wildfire) and frequencies of truffle species, suggesting that disturbance had long-lasting effects on the composition of truffle species (Waters et al. In Press). Other studies have also shown that composition of hypogeous sporocarps varied among stands with different management or natural disturbance histories (Vogt et al. 1981, Luoma et al. 1991, North et al. In Press). Because forest management alters species composition of fungal sporocarps, we wanted to know whether palatability varied among sporocarps of different fungal species for a common, mycophagous small mammal. We designed this study to determine whether northern flying squir-

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rels preferred sporocarps of certain fungal species over others, and secondarily to compare preferences of flying squirrels between fungal sporocarps and other naturally occurring food types.

Methods

Flying squirrels were trapped 4-5 August 1994 in 2 old-growth (>200 years) fir stands in Swain Mountain Experimental Forest, located in Lassen National Forest in northeastern California. Only males were kept for the experiments to control for possible sex effects in food preferences (e.g., the sensory acuity of females may vary according to reproductive status). Squirrels were transported to Humboldt State University in Arcata, California, where they were housed individually in 1.0x1.0x1.5-m outdoor cages. Cafeteria-style experiments were conducted in 2 1.2x1.2x1.0-m cages that had wooden frames and 1-cm hardware cloth sides. Lids were made of clear plexiglass. A wooden tray served as the floor of each cage. Trays were filled to a depth of 6-7 cm with peat moss. The 2 cages were located in separate indoor rooms that lacked windows.

Squirrels were allowed to acclimate to captivity for 2 weeks before experiments began. During the acclimation period, squirrels were fed samples of the food types used during the experiments for approximately 30 minutes each night while in the test cage. Beginning the day before the experiments began, animals were maintained on a reduced diet of rat chow, apples, and water. They were weighed daily to ensure that their weight did not drop below 90% of their capture weight.

Experiments began shortly after sunset when squirrels were moved from their outdoor cages into the test rooms, which were each illuminated with a red light. Order of testing and test room were randomly determined each night. Flying squirrels entered the center of the cage through a plastic tube (8 cm in diameter). An observer recorded behavioral observations with a tape recorder from a blind 1 m from the test cage. Seven squirrels were tested for 45 minutes each night for 4 consecutive nights (17-20 August 1994).

Preferences of flying squirrels were compared among 3 types of food that are available to flying squirrels in the Lassen National Forest: fungal sporocarps, epiphytic lichens, and fir seeds. Fungal sporocarps and lichens were collected in old-growth and mature stands within Swain Mountain Experimental Forest. Fir (*A. concolor* and *A. magnifica*) seeds were obtained from a U.S. Forest Service nursery in Placerville, California. We used sporocarps of 5 species of fungi that were found in sufficient quantities at the time of sampling (14-16 August 1994). Sporocarps were found by raking through the organic layers and upper mineral soil in 4-m^2 circular plots (1.13-m radius) randomly located throughout forest stands. The 5 species were *Gautieria monticola*, *Alpova trappei*, *Gymnomyces abietis*, *Endoptychum depressum*, and *Arcangeliella lactarioides*. *Gautieria monticola*, *Alpova trappei*, and *Gymnomyces abietis* are truffle species; sporocarps lack gills and a stipe and are found below ground. *Endoptychum depressum* and *Arcangeliella lactarioides* are secotioid fungal species, which are considered evolutionary intermediates between fungi that produce epigeous sporocarps and truffles and have morphological and fruiting characteristics of both groups; sporocarps have convoluted gills that are covered by a veil, a reduced stipe, and are found both at the ground surface and below ground. The 2 lichens were *Letharia vulpina* and *Bryoria fremontii*, which were 2 of the most common epiphytic lichens within Swain Mountain Experimental Forest. Fungal sporocarps and lichens were kept in a refrigerator until used in the preference tests.

Size of food samples was standardized across foods and tests; samples were 2-3 cm in diameter. All food samples were weighed before and after each test to determine proportion of food eaten. Each food sample was placed in a randomly assigned grid cell across the tray of the feeding cage before the squirrel entered the cage. Truffles were buried 2-3 cm, and all other samples were placed on top of the peat moss. Fir seeds were placed in a petri dish 4 cm in diameter that was buried so it was level with the peat moss. The peat moss was thoroughly mixed with a rake after each experiment and was changed nightly.

Data Analysis

We compared 3 measures of food preference: (1) proportion of food eaten, (2) number of tests in which food was at least partially eaten, and (3) rank order food was first eaten. Any food types not eaten were ranked last. We used the Spearman rank correlation coefficient for each of the 3 pairwise comparisons of these measures as an index

of similarity. The number of tests in which a food was at least partially eaten was averaged across the 7 squirrels, and proportion of food eaten and rank order food was first eaten were averaged across the 4 nights and 7 squirrels. Ranked correlations ($\underline{n}$ = 8 foods) were high ($\underline{r}_S$ = 0.98 between proportion of food eaten and number of tests food was at least partially eaten, $\underline{r}_S$ = -0.95 between proportion of food eaten and rank order food was first eaten, and $\underline{r}_S$ = -0.98 between number of tests food was at least partially eaten and rank order food was first eaten), indicating the 3 measures provided similar information. We used the proportion of food eaten (averaged across the 4 nights) to test for a difference in food preference among the 8 foods using a randomized complete-blocks (each squirrel was a block) design analysis of variance (ANOVA). Unplanned multiple comparisons were performed using the Ryan-Einot-Gabriel-Welsch multiple-range test (SAS Institute Inc. 1989:947). Roa (1992) and Manly (1993) proposed using multivariate analyses of data from food-preference experiments where foods are presented simultaneously because of the lack of independence among foods. We decided to use a more simple univariate approach because the food samples provided were small (2-3 cm in diameter), so consumption of 1 food probably had little effect on consumption of other foods.

Results and Discussion

Mean proportion of food eaten varied significantly among the 8 foods ($\underline{F}_{7, 42}$ = 31.75, $\underline{P}$ < 0.001). Multiple comparisons indicated that the truffle species *Gautieria monticola* was eaten significantly more than the truffle species *Gymnomyces abietis*, and the secotioid species *Endoptychum depressum* was eaten significantly more than the secotioid species *Arcangeliella lactarioides* (Figure 1). Among the 5 species of fungi, mean proportion of food eaten ranged from 0.90 (s.e. = 0.05) for *Gautieria monticola* sporocarps to 0.11 (s.e. = 0.04) for *Arcangeliella lactarioides* sporocarps.

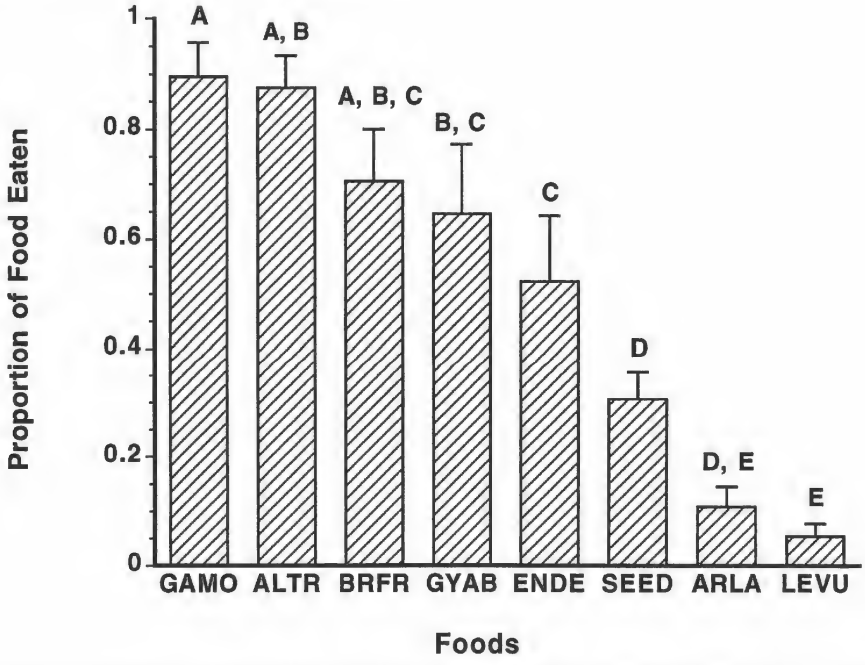

Figure 1. Means and standard errors of proportion of food eaten (averaged across a 4-night period) by 7 captive, male northern flying squirrels during cafeteria-style feeding trials. Foods were *Gautieria monticola* sporocarps (GAMO), *Alpova trappei* sporocarps (ALTR), the lichen *Bryoria fremontii* (BRFR), *Gymnomyces abietis* sporocarps (GYAB), *Endopytchum depressum* sporocarps (ENDE), fir seeds (SEED), *Arcangeliella lactariodes* sporocarps (ARLA), and the lichen *Letharia vulpina* (LEVU). Foods with the same letter did not differ significantly using the Ryan-Einot-Gabriel-Welsch multiple-range test.

The 3 truffle species were consumed more than the 2 secotioid species, which is consistent with results of other studies that showed hypogeous sporocarps were more common in the diets of mycophagous small mammals than were epigeous sporocarps (Maser et al. 1978, 1986, Ure and Maser 1982, Maser et al. 1985, Maser and Maser 1987, Taylor 1992). Our results are also consistent with 3 studies that found that spores of *Gautieria* and the *Rhizopogon* group, which includes the genus *Alpova* (Castellano et al. 1989), were the most common truffle spores identified in northern flying squirrel stomachs and fecal pellets in Oregon and California (Maser et al. 1985, Maser et al. 1986, Hall 1991). Hall (1991), whose study was conducted in the northern Sierra Nevada not far from our study area, found that *Gautieria* spores were found in 87% of 107 flying squirrel fecal pellets and stomachs examined, the *Rhizopogon* group in 81%, and the *Martellia* group, which includes the genus *Gymnomyces* (Castellano et al. 1989), in 17%. Maser et al. (1985) also found that the *Martellia* group was less common than *Gautieria* and the *Rhizopogon* group, and Maser et al. (1986) did not record the presence of the *Martellia* group.

The lichen *Bryoria fremontii* was ranked third in mean proportion of food eaten. The relatively high preference for this lichen is consistent with dietary studies, which have shown that lichens were common in the diets of northern flying squirrels (McKeever 1960, Maser et al. 1985, Maser et al. 1986, Hall 1991). These studies, however, showed that lichens were much less common in the summer diets of flying squirrels than the winter diets, suggesting that lichens were eaten primarily when other foods like truffles were unavailable. Because our study was only conducted during the summer, we cannot assess potential differences in food preferences among seasons. The small amounts of the lichen *Letharia vulpina* eaten is not surprising because this species contains vulpinic acid, which is thought to be toxic to mammals (Smith 1921, Rundel 1978).

Flying squirrels ate sporocarps of 4 of the 5 species of fungi and one lichen species significantly more than fir seeds. This is consistent with dietary studies, which have not found conifer seeds to be common in the diets of northern flying squirrels. Brink and Dean (1966) found that red squirrels (*Tamiasciurus hudsonicus*) in Alaska could maintain weight on a diet of white spruce (*Picea glauca*) cones, but northern flying squirrels could not. In our study, fir seeds were not presented on the cone as they would be found under natural conditions. Because the squirrels did not have to extract seeds from the cone, however, the energetic value of the seeds was theoretically greater than the energetic value of fir seeds under natural conditions.

We showed that preference varied significantly among the 8 foods tested, but we do not know how the nutritional and energetic values of these foods varied. Cork and Kenagy (1989) found that the nutritional value of 1 species of truffle (*Elaphomyces granulatus*) was low for the ground squirrel *Spermophilus saturatus* because digestibility of the sporocarps was low. They hypothesized that truffles in general have relatively low nutritional value for small mammals but are commonly consumed because truffles are seasonally abundant and highly detectable due to the strong odors they develop when mature. Claridge and Cork (1994), however, found that the energetic values of 2 truffle species were high for a forest-dwelling marsupial (*Potorous tridactylus*) in Australia. Because of their high water content, fungal sporocarps may be important during certain periods or in certain areas as a source of water (Fogel and Trappe 1978). Additional research will be needed to determine the nutritional values of different truffle species for different species of mycophagous small mammals.

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Temperature Adaptations of Embryos from Intertidal and Subtidal Sand Dollars (*Dendraster excentricus*, Eschscholtz)

Abstract

Animals living in the marine intertidal zone have a suite of adaptations that allow them to survive thermal stresses associated with low tides. We hypothesized that adjustments of adult organisms to their thermal environment might be reflected in the thermal tolerances of their developing offspring (i.e., adults that survive large temperature fluctuations might produce embryos that have similarly large tolerances). Comparison of the thermal biology of developing sand dollar embryos (*Dendraster excentricus*) which were offspring of adults living in intertidal or subtidal habitats revealed subtle differences in effects of temperature on survival and developmental rates. Intertidal and subtidal *D. excentricus* showed similar fertilization success at temperatures from 7° to 19°C and could develop from fertilized egg to pluteus larva at temperatures from 7° to 26°C. Within this common tolerance range, however, subtidal animals' offspring were more likely to develop normally at lower temperatures (8° - 16°C), while the intertidal animals' offspring were more likely to develop normally at higher temperatures (22° - 26°C). There were also significant differences between subtidal and intertidal *Dendraster* groups in the effects of temperature on developmental rates. In particular, cleavage rates of embryos from intertidal adults remained constant or increased as temperature was raised from 7 to 15°C. In contrast, cleavage rates of embryos from subtidal adults decreased with increasing temperature. Ecological observations suggest that these differences are due to physiological acclimatization effects rather than genetic differentiation of the groups. To contrast *D. excentricus* with a different species that is largely confined to subtidal depths, we also examined temperature tolerances of developing sea urchin embryos (*Strongylocentrotus droebachiensis*). We found that its temperature tolerance during early development was slightly narrower and shifted to lower temperatures than that of *D. excentricus*. This correlates well with differences in habitat and reproductive season of these species and may help explain their distributions and abundances.

Introduction

Invertebrates living in the marine intertidal zone can experience enormous changes in their physical environment as they are repeatedly covered and uncovered by tides. Adult organisms living here generally show behaviors that help minimize their exposure to the fluctuations or physiological adaptations that enable them to tolerate the stress. However, factors affecting early developmental stages of intertidal species also critically test adaptation. Temperature is a particularly important environmental parameter because many animals, during early development, are less tolerant of temperature variation than during other parts of their lives (Cossins and Bowler 1987).

Responses of developing embryos to temperature variation have been extensively investigated in echinoid echinoderms. Many early investigations were basic descriptions of effects temperature has on development (for references see Tyler 1936, Hoadley and Brill 1937, Harvey 1956). Subsequent research revealed correlations between responses of developing embryos to temperature and the particular temperatures encountered during the normal breeding season (Andronikov 1975, Amy 1983, Strathmann 1987, Fujisawa 1989, Fujisawa and Shigei 1990). Others have investigated responses of developing embryos to thermal extremes (e.g., Clarke 1982, Bosch et al. 1987, Chen and Chen 1992).

For some species there may be only one characteristic set of temperature responses during development. Members of such species could breed in any given geographic region when environmental temperatures there reach the optimal range for development (Sastry 1975, Marcus 1983). There are, however, reports of intraspecific geographic variation in developmental temperature responses in some echinoids (Fox 1936, Stephens 1972, Strathmann 1987) and other echinoderms (Johnson and Babcock 1994). These geographic differences in effects of temperature on development could result from genetic differentiation of

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populations (Hilbish et al. 1994), physiological acclimatization (Cossins and Bowler 1987), or a combination of the two. In some species with extended breeding seasons or more than one breeding season per year, responses of developing embryos to temperature in a single location can change seasonally (Hørstadius 1975, O'Connor and Mulley 1977). If members of a species breed throughout an extended period in one location, any seasonal changes in temperature tolerances of the embryos are attributable to the parents' physiological response to temperatures (acclimatization). Thermosensitivity of developing embryos is largely or exclusively determined by the egg (maternal acclimatization) and not by the fertilizing sperm (Fujisawa 1993). Maternal effects, resulting in such seasonal changes, have been demonstrated in other invertebrates (Tester 1985, Pedersen and Tande 1992).

Some of the adaptations to temperature seen in echinoid development may be related to variability of the habitats the animals occupy. For example, the especially broad developmental temperature tolerances reported for echinoid species that occur in reef flats (Rupp 1973) or shallow tropical waters that become very warm (Chen and Chen 1992) may be crucial for those species' reproduction, subjected as they are to very large temperature fluctuations.

The sand dollar, *Dendraster excentricus* Eschscholtz, occurs in both intertidal and subtidal habitats. Individuals living in intertidal habitats are exposed to considerably broader temperature ranges than are individuals living subtidally. This provided an opportunity to test the possibility that there is a relationship between parental habitat and temperature tolerance of developing embryos. We did this by comparing the effects of various exposure temperatures on development in *D. excentricus* individuals collected from one subtidal site and several nearby intertidal sites. We also compared effects of temperature on development of *Dendraster* with those on development of *Strongylocentrotus droebachiensis*, an echinoid that breeds earlier in the spring and is largely confined to low intertidal and subtidal habitats.

Methods

Adult temperature environments

Subtidal *Dendraster excentricus* (Eschscholtz 1831) were collected from Deepwater Bay on Cypress Island. Intertidal *D. excentricus* came from East Sound (Orcas Island), from Bellingham Bay, and from Illahee State Park (Fig. 1). Sea urchins, *Strongylocentrotus droebachiensis* (Müller 1776), were collected from Burrows Bay (Fidalgo Island). All collections were made in the months of May, June, and July when the animals were reproductive. Subtidal animals were collected by divers at depths between 15 and 18 m. Animals were kept in flow-through seatables at the Shannon Point Marine Center and, except for those used in acclimation experiments, were used for experiments within five days of collection.

Water temperatures at -1.5 m were measured weekly for one year at Deepwater Bay, the collection site for subtidal *D. excentricus*. This area experiences strong tidal flushing and the waters are well-mixed; strong thermoclines did not seem to develop even in the warmest summer months (pers. obs.). We assume, therefore, that surface water temperatures at this site reflect those experienced by *D. excentricus* at 15-18 m. To document temperature variations experienced by animals at an intertidal site, we measured surface body temperatures of *D. excentricus* at the East Sound collecting site during 2 low-tide series: 14 April (a windy, overcast day, 11°C air temperature) and 25 April (a clear, sunny day, 13°C air temperature). Every 15 minutes throughout the low tide, a thermister probe was placed on the surfaces of 10 arbitrarily chosen animals and their temperatures were recorded.

Fertilization

For all fertilization and development experiments, gametes were obtained by injecting 0.55 M KCl into the perivisceral coelom. Eggs were collected in 13°C filtered seawater but sperm were collected in a dry petri dish and diluted just prior to insemination. To mitigate effects of individual variability, sperm from 2-4 males and eggs from 2-4 females were mixed in all experiments.

To determine whether fertilization is temperature-dependent and differs between intertidal and subtidal *D. excentricus*, we examined fertilization success at a range of experimental temperatures. Five replicate 20 ml scintillation vials were filled with 16 ml of 5 µm-filtered seawater at 7, 11, 15 and 19°C. A monolayer of newly spawned eggs (with no germinal vesicle evident) and 5 drops of diluted sperm suspension (approximately 1.25

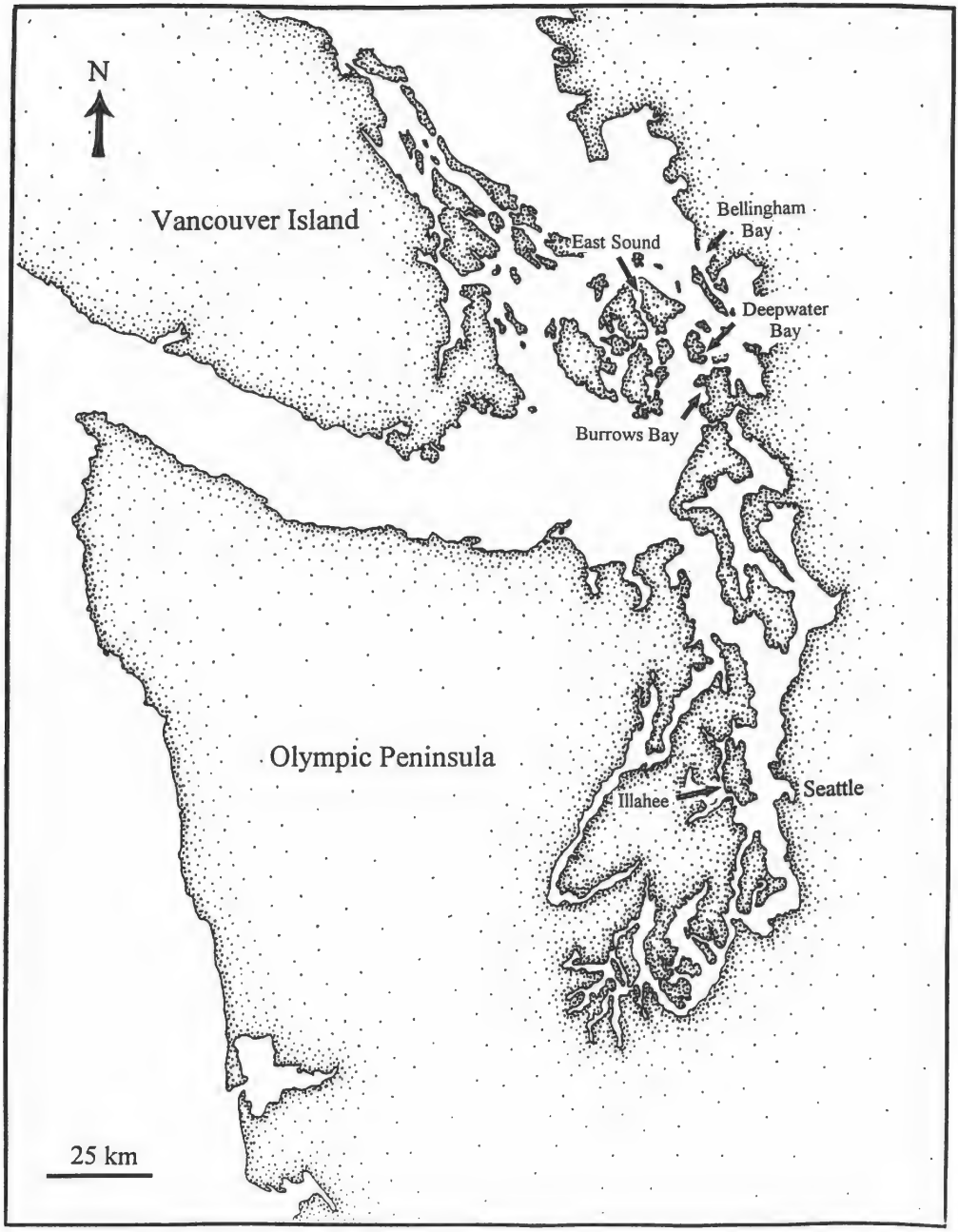

Figure 1. Collection sites: Bellingham Bay, East Sound (Orcas Island), and Illahee State Park where intertidal D. excentricus were collected at low tide; Deepwater Bay (Cypress Island) where subtidal *D. excentricus* were collected; Burrows Bay where subtidal *S. droebachiensis* were collected. All subtidal animals were collected from depths between 15 and 18 m.

$\times 10^5$ sperm per ml) were added to each vial. Contents of the vials were mixed and incubated at the experimental temperatures for 1 hour. Fertilization success was then measured by examining 100-egg samples from each vial for presence of elevated fertilization membranes.

Early development

We also compared effects of temperature on survival of embryos from intertidal and subtidal *D. excentricus*. Batches of eggs were fertilized at an intermediate temperature (13°C) and then transferred to 20-ml scintillation vials. These cultures were maintained in incubators set at 5, 8, 10, 13, 16, 19, 22, 26, 29 and 31°C. All treatments were replicated (4 vials/treatment). Because cultures were unstirred, egg densities were kept low (2-5 eggs/ml). When four-armed pluteus larvae had developed, the cultures were terminated by addition of 4% buffered formalin. All individuals were then examined and the percentages of normal plutei were determined for each vial. The percentage data were arcsine transformed to stabilize variances and treatments were compared with two-way ANOVA with temperature and habitat (i.e., subtidal vs. intertidal) as the main effects.

To contrast *D. excentricus* with another echinoid that seldom occurs intertidally, we also measured temperature tolerance of developing green sea urchin embryos (*S. droebachiensis*). Methods were identical to those described above except that initial fertilization was done in 10°C water.

Early embryonic cleavage rates are generally proportional to rates for longer periods of development (Fujisawa 1989). Therefore, we compared effects of temperature on developmental rates of a subtidal (Deepwater Bay) and 2 intertidal (Illahee State Park and Bellingham Bay) *D. excentricus* groups by measuring early cleavage rates in cultures held at 7 and 15°C. When some embryos in the cultures had reached the 16-cell stage (after 3 hr at 15° and 11 hr at 7°), the cultures were terminated by addition of 4% buffered formalin and cleavage stages of 100 embryos per vial (5 vials per treatment) were recorded. Mean numbers of cleavages completed were calculated and the relationship between number of cleavages and temperature for each group was evaluated with linear regression. Effects of exposure temperature on developmental rate for each group were examined by comparing slopes of the regression lines.

Acclimation

To test effects of recent temperature exposure of parents on development of offspring and to determine whether tolerance limits could be shifted experimentally, we conducted acclimation experiments in which we placed newly collected *D. excentricus* and *S. droebachiensis* in 80-l aquaria adjusted to 7, 10, and 13°C. We defined temperature acclimation as physiological adjustment made by organisms subjected experimentally to environments differing only in temperature. Acclimatization, in constrast, is physiological adjustment made by organisms subjected in the field to a full range of environmental variation. The aquaria were aerated and held in incubators that maintained the acclimation temperatures. Animals were fed every 2 days (TetraMin™ fish food or algae, primarily *Laminaria* spp.) and the water was changed semi-weekly. There were no apparent negative effects of this treatment and animals were successfully made to spawn by injection of 0.55M KCl after a 21-day acclimation. Cultures of embryos were produced as described above and survival to the four-armed pluteus was determined at 5, 7, 10, 13, 16, 20, 24, and 31°C.

Results

Temperature measurements in the field showed that subtidal and intertidal animals experience substantially different temperature regimes. Temperatures in Deepwater Bay ranged from 7°C in January to 13°C in July/August. This seasonal temperature change occurred gradually, and extreme values were rare. In contrast, temperature changes at the intertidal site were more frequent, more sudden, and much greater. Animals in this habitat experienced particularly large temperature fluctuations during low tides; we measured an eight-degree increase (from 13°C to 21°C) in *D. excentricus* body surface temperature during a single 90-minute period (Fig. 2). Mid-summer low tides may expose the animals to even greater fluctuations as air temperatures reach 20-30°C.

We found no biologically relevant among-group differences in *D. excentricus* fertilization success at temperatures from 7-19°C. Fertilization percentages ranged from 90 -100 in all treatments and the only temperature effect seemed to be a slight decrease in fertilization of all groups at 7°C.

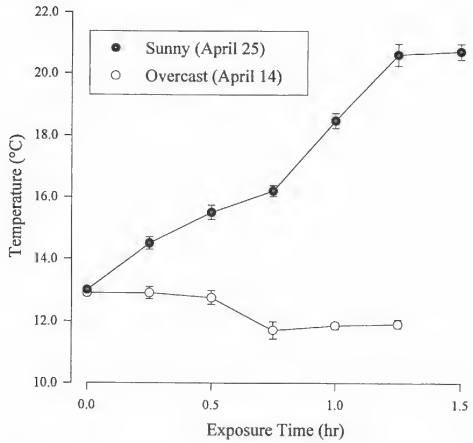

Figure 2. Body surface temperatures of *Dendraster excentricus* measured with a thermister on two low tides (East Sound, Orcas Island). Means ± one standard error are shown (n = 10 for each data point).

Study of developing embryos from both intertidal and subtidal *D. excentricus* at temperatures between 5° and 31° C, revealed that development to four-armed pluteus larvae was normal at temperatures from 7° C to 26° C; there were no significant differences between the two groups in the limits of their temperature tolerance during development. In contrast, the urchin *S. droebachiensis,* which occurs in the same area but is normally found subtidally, developed four-armed plutei across a lower range of temperatures, from 5° to 19°C.

Two-way analysis of variance revealed statistically significant differences, associated with temperature and habitat, between the two *D. excentricus* groups within their common tolerance range (Table 1). Because the significant temperature x habitat interaction made interpretation of the main effects difficult, results were examined through simple main effects (i.e., *Dendraster* groups were compared within each level of temperature, Fig. 3; Winer et al. 1991). With a Bonferroni correction to control Type I error, the analysis showed that a significantly greater proportion of the offspring of subtidal animals successfully completed development to the pluteus stage at lower temperatures (8, 10, 13, and 16°C), whereas a significantly greater proportion of offspring of intertidal animals developed to plutei at the higher temperatures (22 and 26°C).

TABLE 1. Two-way analysis of variance for the effects of temperature and habitat on *D. excentricus* development. Percent data were arcsine transformed prior to analysis to homogenize variances.

Source	df	MS	F	p
Temperature	8	2.775	344.21	<0.01
Location	1	0.095	11.90	<0.01
Temp x Location	8	0.144	17.51	<0.01
Error	54	0.008		
Total	71			

Percentages of normal development, however, were very low in both groups at 26°C (Fig. 3). Temperature tolerance of developing *S. droebachiensis* embryos was shifted to lower temperatures; normal plutei were found in temperature treatments between 5° and 19°C.

The effect of temperature on developmental rates of *D. excentricus* from the subtidal group (Deepwater Bay) differed significantly from that of the 2 intertidal groups (Fig. 4). A significantly negative slope (b = -0.35, p = 0.02) indicated that the Deepwater Bay embryos developed more slowly at 15°C than at 7°C. In contrast, there was no significant temperature effect for the Bellingham Bay group (p = 0.52), and there was a significantly positive effect (i.e., embryos developed more rapidly at 15°C) for the Illahee State Park group (b = 1.01, p = 0.0003).

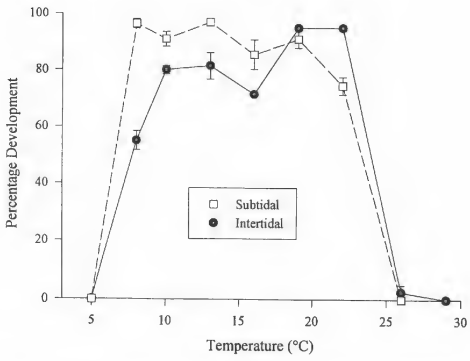

Figure 3. Percentages of intertidal and subtidal *D. excentricus* individuals developing normally to pluteus larvae at various exposure temperatures. Each point represents the mean ± one standard error (n = 4 vials for each point). In several cases, the length of the error bar is smaller than the plotted diameter of the point.

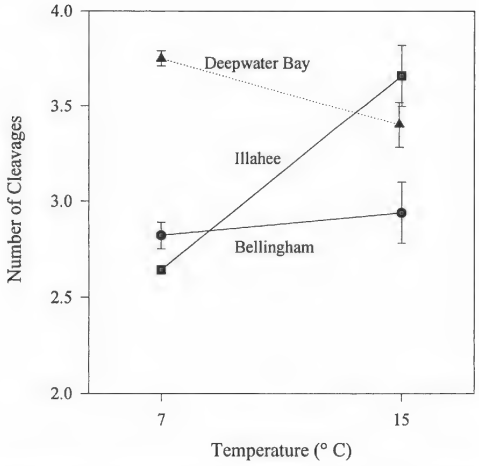

Figure 4. Early developmental rate of intertidal (Illahee and Bellingham) and subtidal (Deepwater Bay) *D. excentricus* as indicated by number of cleavages completed. Each point represents the mean ± one standard error (n = 5 vials for each point).

We found no evidence that a 21-day laboratory acclimation of adult *D. excentricus* or *S. droebachiensis* affects the temperature tolerance of their developing offspring. Survival to pluteus did not differ significantly among the treatment groups for either species; temperature tolerances of the embryos reflected what we had seen in the offspring of unacclimated animals (i.e., Fig. 3).

Discussion

The effects of exposure temperature on *Dendraster excentricus* development suggest a relationship between parental habitat and temperature tolerance of developing offspring. Of particular interest was the drop in cleavage rate we observed for the subtidal *D. excentricus* embryos when they were placed at a warmer temperature (Fig. 4). This was surprising (cleavage rates generally increase with increasing temperature as was more evident in the intertidal groups) and indicates an adjustment to the temperatures embryos are most likely to encounter during early development. Differences in the responses of intertidal and subtidal embryos to temperature could arise from genetic differentiation of populations, from physiological acclimatization, or from a combination of the two. The length of the larval period in *D. excentricus* (10 - 23 weeks at 7 - 13°C; Strathmann 1978) and the high potential for dispersal in the current- and wind-swept waters of the Puget Sound (Emlet 1986) make it unlikely that these differences result from genetic differentiation and suggest that such differentiation might not be adaptive, since larvae would seldom settle in their parents' immediate environment . We think that the observed differences result from a physiological acclimatization effect and could enhance survival of offspring of the respective groups under the conditions likely to be encountered early in development. Laboratory acclimation can alter temperature responses of adult echinoids (Farmanfarmaian and Giese 1963, Ulbricht 1973), and there is evidence that parental acclimatization in nature can shift temperature tolerance of developing embryos in some echinoids (Hørstadius 1975, O'Connor and Mulley 1977, Johnson et al. 1990) and asteroids (Johnson and Babcock 1994). We, however, did not observe any effect of laboratory acclimation on the higher or lower limits of temperature tolerance in embryos of either *D. excentricus* or *S. droebachiensis* nor did we seen any differences in the range of temperatures intertidal and subtidal *D. excentricus* embryos could tolerate. Thus, we do not think that changes in temperature tolerance of embryos occurs simply through a shift in the absolute range of tolerance. Rather, the differences we observed in intertidal versus subtidal *D. excentricus* appear to result from a more complex form of acclimatization involving the relative rotation of developmental temperature response curves (Cossins and Bowler 1987) of the two groups. We suggest that such subtle fine-tuning of responses to environmental parameters during early development is adaptive; it may favor survival of embryos in their earliest, most vulnerable stages. Such a possibility should be further investigated in these, and other, marine organisms.

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Wild Ungulate Influences on the Recovery of Willows, Black Cottonwood and Thin-leaf Alder Following Cessation of Cattle Grazing in Northeastern Oregon

Abstract

Restoration of degraded riparian ecosystems is of great importance for the recovery of declining and endangered stocks of Columbia River salmonids as well as riparian-obligate wildlife species. Willows (*Salix spp.*), thin-leaf alder (*Alnus incana*), and black cottonwood (*Populus trichocarpa*) are important features of western riparian ecosystems having multiple functional roles that influence biological diversity, water quality/quantity, and aquatic/terrestrial food webs and habitats. Removal of domestic livestock and the construction of big game exclosures have been hypothesized to be effective restoration techniques for riparian ecosystem as well as for salmonid habitat recovery. Following more than a century of livestock grazing, cattle were removed from Meadow Creek in 1991 and the rates of riparian shrub recovery were measured for the two years following. Elk and deer-proof exclosures were constructed to quantify the browsing influences of native large ungulates. The initial mean height of 515 deciduous trees and shrubs (14 species) was 47 cm. After two years in the absence of livestock, significant increases in height, crown area, crown volume, stem diameter and biomass were measured both outside and inside of the exclosures. Mean crown volume of willows increased 550% inside of wild ungulate exclosures and 195% outside. Black cottonwood increased 773% inside and 808% outside, while thin-leaf alder increased 1046% inside and 198% outside. Initial shrub densities on gravel bars were low averaging 10.7 woody plants/100m^2. Shrub numbers significantly increased ≈50% (to 15.8 plants/100m^2 m or one new shrub for every 9 meters of transect length) outside of elk and deer proof exclosures through both clonal and seedling establishment. At the beginning of the study (1991), catkin production on willows was low (i.e., only 10% produced catkins). Wild herbivores had a significant influence on the reproductive output of willows; in 1993 catkins were produced by 34% of the tagged willows within exclosures but only 2% outside of exclosures. Wild herbivores were found to have significant influences on the rate of height growth of black cottonwood. For willows, wild herbivores had a significant influence on the rate of growth for the parameters of height, crown area, crown volume, and standing biomass. Nevertheless, due to the inherent resilience and adaptions to natural disturbance processes displayed by the riparian species, there was a rapid and positive response to cessation of those land use activities (i.e, cattle grazing) that caused habitat degradation and/or were preventing recovery.

Introduction

Globally, riparian/aquatic ecosystems are being altered, degraded, or lost at a greater rate than any other time in recorded history and far faster than they are being restored (National Research Council 1992). Degradation of riparian/stream ecosystems by anthropogenic activities along with dams, fishing, and hatchery practices are suggested to have the most pronounced influences on the decline of salmonids in the Pacific Northwest. (Nehlson et al. 1991). In the semiarid forests and rangelands of the Pacific Northwest riparian zones are areas of high biological diversity and productivity (Thomas et al. 1979, Skovlin 1984, Kauffman and Krueger 1984). Records of explorers and fur trappers in the Columbia Basin described the land as abounding with wildlife, and streams rich with salmonids and beaver (*Castor canadensis*) (Thwaites 1905, Rollins 1935, Ogden 1950, Naimen et al. 1988). Streambanks were often noted to be dominated by dense stands of willow *(Salix spp.)*, aspen *(Populus tremuloides)*, and black cottonwood *(Populus trichocarpa)* (Elmore 1992). By the early 1900's, many of these stands had been severely degraded or eliminated in part due to the influences of livestock grazing (Chaney et al. 1990, Elmore and Kauffman 1994, Fleischner 1994). Because cattle (*Bos taurus*) tend to congregate within riparian areas (Roath and Krueger 1982, Gillen et al. 1984), many of these zones have remained overgrazed (Armour et al. 1991, Fleischner 1994). The biological consequences of overgrazing resulting in riparian degradation are disproportionately high because of the diversity

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and large number of aquatic and terrestrial organisms that utilize these ecosystems (Carothers 1977, Thomas et al. 1979).

In the semiarid west, intact riparian plant communities are typically diverse in terms of structure, composition, and edge:area ratios (Kauffman and Krueger 1984). Riparian plant communities are integral to stream function and aquatic productivity (Murphy and Meehan 1991, Swanston 1991, Li et al. 1994). For example, in low-order streams, riparian vegetation strongly influences stream temperature (Li et al. 1994), channel form, habitats of fish and aquatic invertebrates (Sullivan et al. 1986, Sedell and Beschta 1991, Elmore 1992), and are the predominant sources of nutrients and carbon via allocthonous inputs (Cummins 1974). Vegetation also protects streambank soils through root strength, deflection, and dissipation of stream flow energy. Acting as a roughness element, vegetation enhances sediment, debris, and nutrient retention, and hence, channel and floodplain formation (Meehan et al. 1977, Elmore and Beschta 1987, Gregory et al. 1991, Elmore 1992). Riparian vegetation also functions to increase channel diversity and aquatic habitats through creation of overhanging banks and coarse wood debris inputs (Sedell and Beschta 1991, Maser and Sedell 1994).

When livestock or wild ungulates are present during the growing season, the palatable willow or cottonwood shoots are vulnerable to excessive herbivory (Kovalchik and Elmore 1992). In addition, reproduction can be greatly diminished or non-existent when shrubs are repeatedly overgrazed (Kay and Chadde 1992). In Yellowstone National Park, Kay (1994) found a complete absence of catkins on willows which were <2.5m in height and a mean of 670 catkins on plants above this height. Without recruitment or stand establishment, riparian hardwood communities progressively senesce and eventually are eliminated from the ecosystem (Kauffman 1988, Busse 1989, Kauffman et al. 1993). Livestock are a major factor contributing to the decline of riparian communities (Platts 1978, Bull and Skovlin 1982, Fleischner 1994).

In order to survive the high frequency and variable magnitudes of disturbance events, vegetation of riparian ecosystems display adaptations facilitating rapid recovery following such events. A passive restoration approach has been suggested as the logical first step in successful ecological restoration. Passive restoration is defined as the removal of human activities that cause degradation or prevent recovery (Kauffman et al. 1995, Kauffman et al. 1996). Shrub recovery can be dramatic following the elimination of livestock grazing (Platts and Rinne 1985, Elmore and Beschta 1987, Green and Kauffman 1995), but few studies have quantified rates of individual shrub growth, reproductive effort and changes in riparian shrub density when herbivory by cattle, mule deer (*Odocoileus hemionus*) and elk (*Cervus elaphus*) have been eliminated (Crouse and Kindshy 1984, Platts and Rinne 1985).

This project was initiated to improve our understanding of the resilience of riparian hardwoods, in particular the natural ecosystem recovery process following implementation of a passive restoration approach associated with the removal or diminution of herbivore grazing pressure. Our objectives were to quantify rates of shrub growth and re-establishment following the cessation of livestock grazing alone and in combination with the removal of all large animal herbivory. Elk and deer-proof exclosures were utilized to quantify recovery with and without native ungulate influences.

Methods

Study Areas

The study site is located on Meadow Creek, at the Starkey Experimental Forest, Wallowa-Whitman National Forest in the Blue Mountains of northeast Oregon. Meadow Creek is a third order tributary of the Grande Ronde River in the lower Snake River Basin. Elevation of the site is 1130-1400 m. Mean annual precipitation is approximately 60 cm, with two-thirds falling as snow during winter. Stream annual average discharge varies between 0.056 and 5.60 m^3s^{-1}, with annual peaks occurring most often in March, but can occur anytime between January and June (McIntosh 1992). Uplands are dominated by ponderosa pine (*Pinus ponderosa*) and grand fir (*Abies grandis*) on north slopes and by ponderosa pine and bunchgrass communities on the south slopes. Over the 4 km study reach, average channel gradient is 10 m km^{-1} and average sinuosity is approximately 1.13 m m^{-1} (Ganskopp 1978). Gravel bars consisting of coarse to fine-textured alluvium pro-

vide many suitable sites for the potential establishment of willows, thin-leaf alder (*Alnus incana*) and black cottonwood (Busse 1989).

The Meadow creek watershed and riparian zone have experienced a long history of logging, splash dams, roads, railroads, and livestock grazing. At the onset of this study in 1991, Meadow Creek was characterized by a depauperate composition of streambank shrubs and a relatively shadeless, simplified, riffle-dominated channel (Beschta et al. 1991, McIntosh 1992).

Domestic livestock grazing along Meadow Creek began in the 1860's with stocking rates varying between 0.81 ha and 3.0 ha/animal unit month (AUM) until 1975 (Harris 1954, Skovlin 1991). From 1975 until this project began in 1991, utilization levels were maintained at approximately 70% of herbaceous growth with a grazing intensity of 3.2 ha/AUM (Skovlin et al. 1977). Prior to livestock removal, Bryant and Skovlin (1982) reported that shrub utilization was 60 - 65% in all treatments and suggested that elk and deer browsing accounted for about 25% of this impact.

Riparian Vegetation

Planned livestock grazing was terminated along Meadow Creek following the 1990 grazing season. However, some trespass cattle grazed the area each year. Vegetation was measured in 1991 (reflective of a century of livestock grazing), and in 1992 and 1993 (one and two years without livestock).

Annual rates of growth, changes in structure, and reproductive effort were measured on a total of 244 shrubs consisting of 8 species that were permanently tagged and mapped. Measurements included height, elliptical crown area, number of basal stems, and mainstem diameter at the soil surface. Elliptical crown area (A) was calculated utilizing the formula:

$$A = (\pi \times w_1 \times w_2) / 4$$

where w_1 is the maximum crown diameter and w_2 is the perpendicular diameter at its midpoint. Crown volume was calculated by multiplying the elliptical crown area by height. Herbivory by beaver, insects, and large herbivores (deer and elk) was also recorded for each individual. All measurements were taken in late June each year.

Density and establishment rates of riparian hardwoods were quantified through measurement of 52 permanent belt transects that were 2 x 25 m in size. These permanent transects generally paralleled the stream course on gravel bars that are typical of habitats occupied by members of the Salicaceae (Busse 1989). The species and height of all shrubs within the transects were recorded. All field measurements were made from late June to early July each year.

In the Fall 1991, three large game exclosures were constructed on the upper, middle, and lower end of the study site. This allowed for the quantification of shrub growth with and without the influence of large herbivores. One fourth of all tagged shrubs (n=62) occurred within the elk exclosures. Eight of the 52 transects occurred within the exclosures.

Standing biomass and rates of accumulation were calculated from predictive equations developed specifically for these riparian shrubs and trees (Case 1995). Differences in shrub crown area, crown volume and biomass (inside the exclosures vs. outside) were tested using a co-variate analysis of variance with log transformed variables. Crown volume was used as the co-variate; significance levels were set at $p<0.10$. Between treatment comparisons of height, mainstem diameter, and number of stems were determined using analysis of variance with untransformed variables. Between years analyses of individual species characteristics were conducted using paired *t*-tests. Between year changes in density (transect data) were also tested using the paired *t*-test.

Results

Initial Shrub Composition and Stature

In 1991, a depauperate riparian composition and structure reflected a century or more of heavy utilization by domestic livestock. The initial mean height of the 244 tagged individual shrubs (8 species) was 57 cm. The mean width of black cottonwood exceeded its mean height (44 cm and 35 cm, respectively). The mainstem diameter and the general structure of the plants indicated that the majority were not seedlings, but individuals maintained in a low stature by grazing for many years. Sandbar willow *(Salix exigua* var. *melanopsis)*, Mackenzie willow *(S. rigida* var. *mackensieana),* and Booth willow (*S. boothii)* were the most abundant of the tagged willows (Table 1). The structure of willows (i.e., height, and crown volume) also reflected extreme utilization by grazing animals (Figures 1 and 2).

TABLE 1. Change (%) in height, crown area, crown volume, mainstem diameter, number of stems and biomass for thin-leaf alder, black cottonwood, and willows outside (Out) and inside (In) of elk and deer exclosures at Meadow Creek following the termination of livestock grazing (1991-1993).

Species	Sample size		Height		Crown Area		Crown volume		Mainstem Diameter		Number of Stems		Biomass	
	Out	In	Out	In	Out	In	Out	In	Out	In	Out	In	Out	In
Thin-leaf alder	27	4	46*	129*	112*	405*	198*	1046*	46*#	105*	43*	-5	152*	422*
Black cottonwood	23	17	72*#	151*	268*	248*	808*	773*	59*	59*	35*	23	568*	316*
Willows combined:	117	41	18*#	86*	132*#	228*	195*#	550*	44*	38*	49*	49*	235*#	439*
Coyote willow	8	16	2#	102*	30#	303*	47 #	705*	21#	42*	57	75*	48 #	745*
Sandbar willow	29	5	3 #	59*	87*	63*	97*	122*	53*	62*	65*	100*	84*	131*
Whiplash willow	18	7	33*	56*	194*	133	260*	263*	77*	54*	68*	37	358*	216*
Lemon's willow	5	—	2	—	138*	—	153	—	30*	—	71	—	105	—
Mackenzie willow	33	2	14*	107*	106*	175*	161*	488*	49*	36	58*	58	415*	606*
Booth willow	38	11	37*#	80*	159*#	240*	270*	586*	38*	20*	15#	18*	157*#	239*

A superscripted * indicates a significant difference between years (1991-1993), but within the treatment. A superscripted # over data in the Out column indicates a significant difference in total growth when comparing plants inside and outside the exclosures ($p<0.10$).

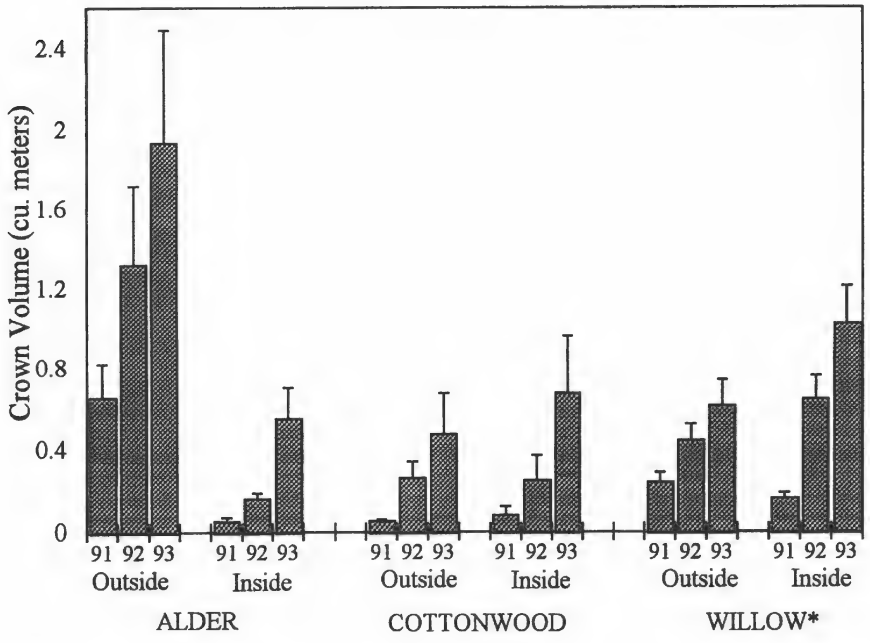

Figure 1. Mean crown volume outside and inside exclosures following livestock removal at Meadow Creek, Oregon (1991-1993). Thin bars represent one standard error. An asterisk (*) indicates a significant difference in growth outside (out) vs. inside (in) of elk and deer proof exclosures.

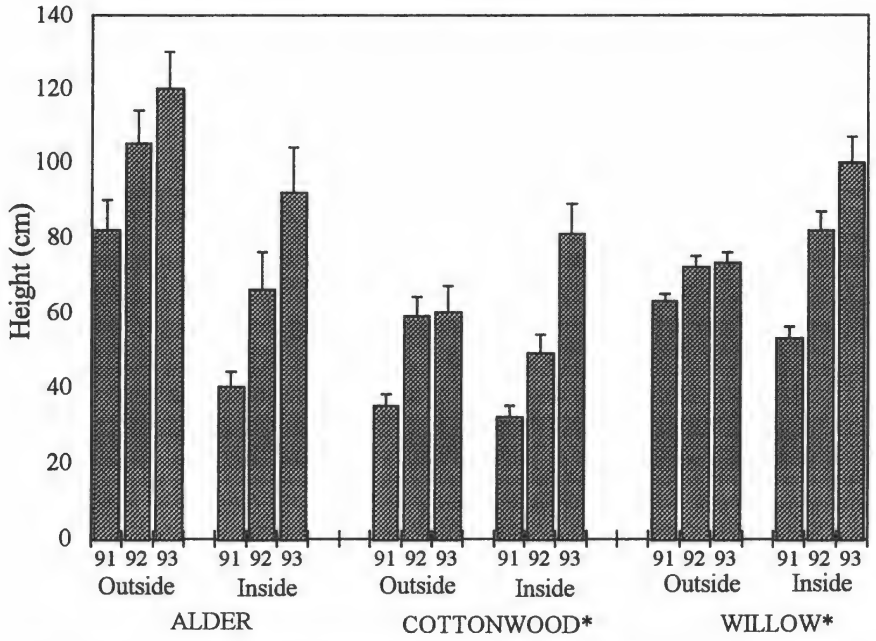

Figure 2. Mean height of thin-leaf alder, black cottonwood, and willow spp. outside and inside of exclosures following the cessation of livestock grazing at Meadow Creek, Oregon. Thin bars represent one standard error. An asterisk (*) indicates a significant difference ($p<0.10$) in height growth 1991-1993 outside vs inside of exclosures.

Initial shrub densities in 52 gravel bar transects was low with a mean of 10.7 plants/100m^2 (a range in density of 0-102 plants/100m^2). Only eight transects had densities >20 plants/100m^2. Density of all willows combined was 6.7 /100m^2, while density of black cottonwood and thin-leaf alder was 1.3 and 1.0 /100m^2, respectively. Density of all other species combined was 1.6 plants/100m^2) (Table 2).

Influences of Wild Herbivores on Riparian Shrubs

Initial shrub responses were dramatic following the removal of livestock but with the continued presence of wild ungulates. For thin-leaf alder, black cottonwood, and willow species combined, all of the measured shrub parameters (except the number of stems) significantly increased from 1991 to 1993. At the beginning of the study, mean biomass of thin-leaf alder, black cottonwood, and willow species outside of elk exclosures was 343 g, 38 g, and 84 g, respectively. Two years following the removal of livestock, increases in biomass ranged from 48% to 568% outside of exclosures and from 131% to 745% inside exclosures (Table 1). During this same time period, shrub crown volume increased 47-808% for all tagged species outside of exclosures (Table 1). Within the exclosures, the range in crown volume increase by species was 122-1046% (Table 1). Small shrubs displayed proportionately greater increases than larger shrubs, and for this reason a crown volume co-variate was used for between treatment analyses (inside vs outside of exclosures). Browsing by large ungulates was apparent on 72% of the tagged shrubs in 1992 and 73% in 1993.

There were significant differences in both the annual height growth and total height for willows and black cottonwood comparing inside and outside exclosures (Table 3 and Figure 2). In two years, black cottonwood within exclosures increased ≈50cm (151%) in height. Outside of exclosures cottonwood height increases were ≈25cm (72%). From 1991 to 1993, the mean height of willows increased from 63 to 73 cm outside exclosures and from 53 to 100cm inside of

TABLE 2. Shrub density on gravel bars at Meadow Creek, Oregon (1991- 1993). Numbers are mean and standard error (in parenthesis). Taxonomy follows that of Hitchcock and Cronquist (1973) and Brunsfeld and Johnson (1985).

	Density (#/100m^2)		
Species	1991	1992	1993
Thin-leaf alder *(Alnus incana)*	0.96 (0.22)	1.19 (0.39)	1.58 (0.47)
Black cottonwood (*Populus trichocarpa*)	1.28 (0.67)	1.88 (0.78)	2 (0.94)
Coyote willow *(Salix exigua* var. *exigua)*	0.28 (0.17)	0.62 (0.33)	0.69 (0.41)
Sandbar willow *(Salix exigua* var. *melanopsis)*	5.00 (2.40)	6.23 (2.98)	6.96 (3.25)
Pacific willow *(Salix lasiandra var. caudata)*	0.16 (0.08)	0.38 (0.12)	0.38 (0.12)
Lemon's willow (*Salix lemmonii*)	0.04 (0.04)	0.04 (0.04)	0.04 (0.04)
MacKenzie willow (*Salix rigida var. mackenzieana*)	0.52 (0.17)	0.77 (0.23)	0.58 (0.18)
Booth willow *(Salix boothii)*	0.88(0.24)	0.81 (0.23)	0.88 (0.26)
Red-osier dogwood *(Cornus stolonifera)*	0.12 (0.09)	0.15 (0.17)	0.15 (0.09)
Black hawthorn (*Crataegus douglasii*)	0.12 (0.12)	0.15 (0.09)	0.12 (0.11)
Stinking currant (*Ribes hudsonianum*)	0.92 (0.46)	0.96 (0.15)	1.38 (0.51)
Common snowberry *(Symphoricarpos albus)*	0.36 (0.22)	0.58 (0.27)	0.88 (0.37)
Wax currant (*Ribes cerum*)	0.04 (0.04)	0.15 (0.32)	0.04 (0.04)
Pearhip rose *(Rosa woodsii)*	0.04 (0.04)	0.15 (0.15)	0.12 (0.08)
Service berry *(Amelanchier alnifolia)*	0	0.04 (0.11)	0.04 (0.04)
Red Raspberry (*Rubus idaeus*)	0	0.04 (0.04)	0
Totals	10.72	14.14	15.84

TABLE 3. Mean height growth (cm) during 2 seasons outside and inside of elk/deer exclosures, at Meadow Creek in northeast Oregon. Numbers in parenthesis are standard errors.

SPECIES	1991-1992		1992-1993	
	Outside	Inside	Outside	Inside
Thin-leaf alder	23 (3)	26 (9)	15 (4)	25 (6)
Black cottonwood	24 (4)	17 (4)	1 (5)	31 (5)*
Willow spp.	10 (2)	28 (3)*	1 (2)	18 (4)*
All spp. combined	13 (2)	25 (3)*	3 (2)	22 (3)*

*Indicates a significant difference inside vs. outside of exclosures ($p<0.10$)

exclosures (Figure 2). In addition, for willows we detected significant differences in the increases of crown area, crown volume and biomass between plants outside and within exclosures. The average biomass of all willows combined increased 439% (a range of 80- 439 g) inside the exclosures and 235% (83-178 g) outside of exclosures. Increases in crown volume of all willow species combined was 550% inside and 195% outside of exclosures. Crown volume of thin-leaf alder increased 198% outside of exclosures but 1046% inside the protected exclosures. The small sample size for thin-leaf alder inside the exclosures limited statistical interpretation. Black cottonwood crown

volume growth was 808% outside and 773% inside exclosures during the 2 year period (Table 1).

Individually, coyote willow (*Salix exigua* var. *exigua*), and Booth willow were significantly influenced by wild ungulates for the variables of height, crown area and biomass (Table 1). For example, the increase in average biomass of Booth willow from 1991 to 1993 was 65 to 168 g/plant out of exclosures, and 91-308 g in the exclosures (an increase of 157% and 238%, respectively).

Rates of Establishment, Densities, and Seed Production

Two years following the removal of livestock, the total number of all shrubs encountered in all transects increased by 50% (i.e., from 271 in 1991 to 412 in 1993). This is equivalent to a one new shrub for every 9 meters of transect length. The greatest measured increase was for sandbar willow; 25% of the 144 new plants were of this species. Sandbar willow, which had the highest density of all species on the transects, increased from 5 to 7 plants/100m^2 (Table 2). Individuals from this species can readily establish from stems deposited on gravel bars during high flows. In addition, it was one of the few shrub species that commonly produced catkins (Table 4). The second most abundant species was black cottonwood which increased from 1.3 to 2.0 plants/100m^2, while the third most abundant, thin-leaf alder increased from 0.9 to 1.5 plants/100m^2. All other shrub species combined increased ≈0.5 plants/100m^2.

Most of the increases in density of individual species occurred within the same transects in which they were originally encountered; the increases in the frequency of species (i.e., the percent of transects in which individual species occurred) were slight following two years of grazing cessation. Sandbar willow occurred on more transects than any other (36% in 1991 and 38% in 1993). Frequency of thin-leaf alder was 24% in 1991 and increased to 29% by 1993. Black cottonwood occurred in 20% of the transects in 1991 and did not change during the 2 years. Frequency of whiplash willow (*Salix lasiandra var. caudata*) increased from 8% to 17%, and other willows showed no, or only slight increases or decreases in frequency of occurrence. Other common shrubs which increased in frequency included stinking currant (*Ribes husonianum*) (an increase from 20% to 28%), and common snowberry (*Symphoricarpos albus*), (an increase from 8% to 14%).

TABLE 4. Number of willow plants producing catkins at Meadow Creek, Oregon from 1991-1993.

	1991	1992	1993
Sandbar willow	5	8	4
Coyote willow	8	9	10
MacKenzie willow	1	2	2
Watson's willow	1	0	0
Whiplash willow	1	2	1
Total	16	20	17
% of all willows	9.2	11.4	9.8
Mean # catkins/plant	55 (16)	164 (48)	135 (32)

Limitations to shrub recovery may partially be explained by a lack of reproductive vigor; only 10% of willows produced catkins following livestock removal (Table 4). Sandbar willow and coyote willow were the most prolific making up 80% of the individuals that produced catkins. Of the individual plants that produced catkins, the mean number per plant increased three-fold from the first season (i.e., 55/plant in 1991 to 164 and 135/plant in 1992 and 1993). Most of the reproductive individuals in 1993 were inside of the exclosures; 34% of the willows inside exclosures produced catkins as compared to 2% outside of exclosures. From 1991 to 1993, the mean number of plants producing catkins outside of exclosures decreased from 6 to 3 while the number inside exclosures increased from 9 to 14.

Other ecosystem factors influencing shrub recovery included beaver which removed mainstems from 20% of willows, 11% of alder, and 4% of cottonwood during the study (Figure 3). Because they tend to remove the largest of stems, the magnitude of regrowth both within and outside of exclosures was likely diminished by their influences. High flows had discernable negative influences on the growth of 6% of the tagged shrubs in 1993.

Discussion

Interactions between biotic, hydrologic, and geomorphic features determine the rate of riparian recovery following natural or anthropogenic disturbances (Kauffman et al. 1996). On Meadow creek, these ecosystem features have been

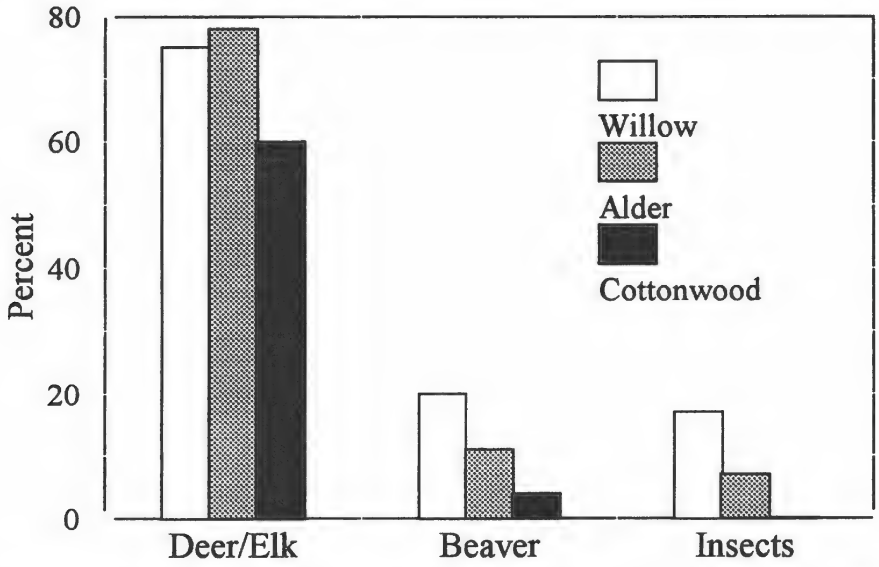

Figure 3. The percentage of individual shrubs browsed by deer and elk outside exclosures in 1993, and the percent browsed by beaver and insects outside during the 1991-1993 period at Meadow Creek.

dramatically influenced by the long period of heavy livestock use as well logging, roads, and other land use activities (McIntosh 1992). Results of these ecosystem perturbations are manifested in incised channels, simplified channel morphology, and changes in hydroperiod (Beschta et al. 1991, McIntosh 1992). A biotic disequilibrium was reflected in the depauperate riparian plant composition and structure (Tables 2, and Figures 1 and 2) as well as high densities of wild herbivores (B. Johnson, USFS La Grande, Oregon, personal communication). These physical and biotic features can combine to retard the restoration process. Nevertheless, significant increases in both the structure and density of the riparian hardwood component has occurred after only two years in the absence of livestock use.

While a 50% increase in shrub density may initially appear to be indicative of successful recovery following the cessation of livestock grazing, this increase must be viewed in terms of the very low initial densities. Density of black cottonwood, thin-leaf alder and willow species in 1993 was 2.0, 1.6, and 9.5/100m^2, respectively at Meadow creek. In contrast, density of these same species in a lightly grazed or cattle-excluded reach of Catherine creek (also an upper tributary of the Grande Ronde River, Northeast Oregon) was 35, 6, and 176 /100m^2, respectively (Green and Kauffman 1995). Irvine and West (1979) also reported similar high densities of Fremont cottonwood (*Populus fremontii*, ≈80/100m^2) and coyote willow (≈260/100m^2) in intact riparian ecosystems of Southeastern Utah.

Recovery of disturbance-dependent riparian shrub communities is a function of seed production or vegetative establishment from stem deposition in suitable substrates (Busse 1989, Kauffman et al. 1985). At the onset of the study, neither of these reproductive processes were occurring in measurable amounts at Meadow creek. The low total aboveground biomass of riparian shrubs as a result of livestock utilization would not have resulted in an abundant source of stem materials for vegetative establishment following flood deposition. In addition, only 10% of the willows produced catkins. Similarly, at Yellowstone National Park, Wyoming, catkin production only occurred on willows above the height of browsing animals (wild ungulates) (Kay 1994). On Meadow Creek, the increase in catkin production in exclosures and the increases in aboveground biomass following cessation of livestock grazing indicates a greater potential for increased rates of willow establishment in the future. For example, in areas with abundant seed and stem sources that were

ungrazed by domestic livestock for 10 years, densities of willows and thin-leaf alder increased by 3 and 7-fold, respectively (Green and Kauffman 1995).

Over-utilization by domestic livestock resulting in the degradation of riparian and stream ecosystems is among the most significant threats to biological diversity in the western USA (Cooperider 1990, Kauffman and Krueger 1984, Fleischner 1994). A passive restoration approach which is simply the removal of those anthropogenic perturbations that are causing degradation or preventing recovery has been suggested to be the first necessary step in ecological restoration and probably the most important (Kauffman et al. 1995). The passive restoration approach in this study was the removal of high levels of herbivory by large ungulates which limited individual stature, reproduction, and establishment. The significant growth response of all hardwood species in the absence of cattle and/or wild ungulate herbivory is indicative of the success of this approach.

Similar responses of riparian vegetation to the removal of livestock has been recorded throughout the west (Crouse and Kindshy 1984, Platts and Rinne 1985, Busse 1989). In cattle exclosures on Catherine Creek, Oregon, height increases for willows and black cottonwood were 100 cm over a 10 year period, while thin-leaf alder increased 200 cm (Green and Kauffman 1995). In our study, the strongest height response was from black cottonwood protected from wild ungulates (i.e., a mean height growth of 31 cm in one season, 1992-1993) (Table 3). Some individual cottonwoods were observed to have grown >100 cm in a single season. In Utah, Behnke and Raleigh (1978) recorded height growth of willows at 50 cm after four years (12.5 cm/yr). In Montana, sandbar willow, a prolific sprouter, quickly re-established where it had not been totally removed by grazing (Hansen 1992). Also in Montana, shrub production was found to be 13 times greater inside of livestock exclosures (Marcuson 1977). Shrub canopy cover in north central Colorado was 8.5 times higher in protected areas (Schultz and Leininger 1990). In south central Washington after 10 years protection from livestock, woody plants had increased in stature and density to form a more or less continuous tree corridor along the entire length of the stream (Rickard and Cushing 1982).

Overuse of shrubs by wild ungulates can be severe when natural processes such as migration or predation are altered, or when management results in animal densities (domestic and native grazers) that are beyond the carrying capacity. It has been suggested that high densities of elk have reduced willow and cottonwood stands by 90% over the past decades in Yellowstone National Park (Kay 1994). In contrast, other studies reported that large wild ungulates had a minor influence on riparian shrub structure (Platts and Raleigh 1984). Rickard and Cushing (1982) and Green and Kauffman (1995) reported increased stature and density of woody plants when livestock were excluded but with the continued presence of wild herbivores.

Wild ungulates along Meadow Creek did influence early recovery after livestock were removed. Mean annual height growth of species outside of exclosures from 1991-1992 ranged from 10-24 cm (Table 3). During the second season (1992-1993) wild ungulate impacts were more severe, reducing height growth for willows and cottonwood to 1 cm. Height growth inside exclosures during this year was 18-31cm. However, crown volume and biomass are better indices to overall growth since they quantify the three-dimensional changes in shrub stature (Table 1 and Figure 1). In terms of total crown volume growth over two seasons, black cottonwood increased 773% inside elk exclosures and 808% outside, while willows increased 550% inside and 195% outside.

Our results may be a reflection of the high densities of deer and elk on the Starkey Experimental Forest (≈5/km^2 for deer and 6/km^2 for elk). In addition, natural migrations have been altered through construction of the 77 km^2 big game enclosure surrounding the Experimental Forest. Because Meadow Creek is the only area not utilized by cattle within this enclosed area, wild ungulate influences on the riparian zone may be higher than would occur if cattle densities were lower throughout this forest.

We found that elk and deer use had greater influences on willows and black cottonwood than on thin-leaf alder. This preference for willows may be partly explained by its higher nutrient concentrations. Foliage of coyote and sandbar willow were found to contain higher concentrations of crude protein with a lower C:N ratio than black cottonwood or thin-leaf alder (Case 1995). Others have also reported that willows and cottonwood were preferred over alders (Kufeld 1972).

Conclusion

Many riparian zones in the west have been degraded since Euro-American settlement with deleterious consequences for fish, wildlife, and water quality. The continuous grazing effects of domestic livestock along with wild herbivore influences resulted in the degradation and/or have prevented the recovery of many western riparian systems. Because traditional livestock grazing strategies have focused on the ecology and production of upland communities, riparian/fisheries and wildlife values have often been overlooked (Wagner 1978, Nehlsen et al. 1991, Fleischner 1994). As in many other riparian zones of the interior west, the riparian-obligate hardwoods along Meadow Creek were all but eliminated. Given their value as providing critical habitat features for both the terrestrial and aquatic biota of these ecosystems, improved riparian management and ecological restoration are in need of implementation.

Riparian ecosystems are zones of frequent and varied disturbances at many temporal and spatial scales (Gregory et al. 1991). It was hypothesized that vegetation recovery following cessation of high intensities of grazing would be rapid in riparian ecosystems because of available water and nutrient resources, and because of the inherent plant adaptations for survival following frequent natural disturbances. We used a passive restoration approach and examined the inherent resilience and early regrowth responses following the removal of livestock, with and without wild ungulate browsing. Following more than a century of heavy grazing, growth increases were dramatic. However, wild herbivores had significant and negative influences on the rate of recovery on the height of black cottonwood, and height, crown area, crown volume, biomass and reproductive output of willows.

The rates of establishment were low at Meadow Creek due to the scarcity of mature-statured shrubs and the absence of reproduction. Nevertheless, the total number of all shrubs combined increased 50% in two seasons. If this trend continues artificial plantings will be unnecessary. We expect that as stature and vigor increase, more shrubs will produce seed and densities will continue to increase.

The restoration of endangered fisheries is a great concern for many western stream/riparian ecosystems (Nehlsen et al. 1991, Frissell 1993). Watershed and aquatic habitat restoration and sustainability include the re-establishment of streamside plant communities which provide many essential ecological functions. Over browsing by herbivores can severely reduce seed production, plant establishment, and plant vigor/survival. Due to their accessibility and palatability, recovering low-profile shrub communities remain vulnerable when herbivores are present. Although light seasonal livestock grazing in some systems may be compatible with some objectives, complete protection during the first 5-10 years of recovery offers the greatest likelihood of successful restoration (Kovalchik and Elmore 1992, Elmore and Kauffman 1994, Fleischner 1994). Where elk and/or deer populations are high, and the most rapid riparian recovery possible is desired, additional protection measures may be required at least during the initial recovery period.

Acknowledgments

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An Increase In Herbivory of Cottonwood in Yellowstone National Park

Abstract

This study examined an effect of elk (*Cervus elaphus nelsoni*) on narrowleaf cottonwood (*Populus angustifolia*) in northern Yellowstone National Park, where stands consist of old trees and younger, densely-branched bushes. The elk herd increased from a census of 3,172 in 1968 to a census of 18,913 in 1988. The purposes of this study were to: 1) document the height-growth of cottonwood bushes, 2) determine if the height of browsing corresponded with snow depth, and 3) determine if there has been a recent increase in cottonwood herbivory. In 5 stands of different age (ranging ca. 9-45 y old), I measured the height of live previous-year-growth and the height of the oldest stems killed by browsing. The tallest previous-year-growth was 80 cm; all stems taller than 29 cm had been browsed. Stems were killed by browsing closer to the ground in younger stands (respectively, 87, 62, 28, 14, and 9 cm; $P < 0.001$). There was no change in mid-winter snow depth during the period 1950-1994. The 2 stands established since 1977 had relatively small variances in the height at which stems were killed by browsing (21 and 15 cm^2), a uniformity likely caused by intense herbivory since respective stand creation. The large variances in the height of browse-killed stems in older stands (745, 399, and 291 cm^2) were likely caused by an initial period of light-to-moderate herbivory followed by an increase in herbivory that killed the stem tips at the heights existing at the time. The bush growth-form apparently results from an increase in herbivory that occurred between 1968 and 1977, a period in which the elk winter census increased from 3,172 to 8,981. The weight of evidence suggests that EuroAmerican influences have caused the northern elk herd to increase in number since the establishment of the park. If herbivory does not decrease, cottonwood may be eliminated from Yellowstone's northern range.

Introduction

Over the past century, the elk (*Cervus elaphus*) population of northern Yellowstone National Park (YNP) has fluctuated in number. In response to studies that indicated range damage due to overgrazing (Wright and Thompson 1935), the herd was culled from 1935–1967 (Houston 1982). By 1968, the population declined to a low census of 3,172. Following the halt of the reduction program in 1968, the herd increased to a high census of 18,913 in 1988 (Coughenour and Singer 1996). The current condition of the northern range has become controversial (Chase 1987, Wagner et al. 1995).

There has been general agreement that some species of browse have declined since the establishment of YNP. Singer and Renkin (1995) reported a decline in big sagebrush (*Artemisia tridentata*) at lower elevations of the northern elk winter range. Kay and Chadde (1992) and Singer et al. (1994) reported the decline of willow (*Salix* spp). A decline of aspen (*Populus tremuloides*) was documented by Kay (1990, 1993) and Romme et al. (1995).

The effect of herbivory on other common browse plants such as birch (*Betula* spp.), alder (*Alnus* spp.), and chokecherry (*Prunus virginiana*) has not been formally documented, however, the hedge-like appearance of young plants attests to significant herbivory. In areas where elk feed during the winter, lodgepole pine (*Pinus contorta*) and Douglas fir (*Pseudotsuga menziesii*) that are about 10 - 15 years of age have the following growth form: stems ca. 1–1.5-m tall have live branches from 0 – ca. 0.4 m above ground level, the remainder of the stem being dead. Bite marks indicate that the upper stem was killed by browsing. The live foliage on the lower stem is apparently protected by snowcover. Older conifers are highlined, while younger plants are browsed to hedge-like bushes 20–40 cm tall.

There is disagreement on the cause of the declines. Proposed explanations can be placed into three general categories: 1) the declines are due to past fire suppression (Houston 1982, Despain et al. 1986), 2) the declines are due environmental change (Singer et al. 1994), and 3) the declines are due to EuroAmerican influences (Smith et al. 1915 unpub. rep., Graves and Nelson 1919, Cahalane 1941, Kay 1990). To be generally accepted, an explanation should account for the level of herbivory experienced by all browse species growing on the northern range.

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The purpose of this study was to examine the effect of herbivory on narrowleaf cottonwood (*Populus angustifolia*) in northern YNP. Narrowleaf cottonwood is a riparian tree that grows to 20 m tall (Harrington 1964). Establishment from seed is usually limited to the moist zone at the edge of streams, therefore, stands of different age often record a history of channel migration (Everitt 1968, McBride and Strahan 1984). Once established, recruitment from suckers is common (pers. obs.).

Herbivory can alter the form and size of woody plants. In some species, clipping initiates clusters of twigs at the ends of shoots (Cole 1958, Ferguson and Basile 1966, Riney 1982). Height growth may be inhibited (Gaffney 1941, Harlow and Downing 1968, Ross et al. 1970, Olmsted 1979). Intense herbivory may kill the top of a plant and cause young shoots to originate from the surviving lower stem (Garrison 1953, Patten 1968).

Snow depth influences the feeding behavior of elk (Nelson and Leege 1982, Skovlin 1982) and a change in snow depth could plausibly alter the height at which plants are browsed. An increase in herbivory could also affect the height at which stems were browsed. If, during a period of light herbivory, plants grow to heights that approximately correspond with age, an increase in herbivory could logically cause the stem tips of younger (shorter) plants to be browsed closer to the ground compared to the stem tips of older (taller) plants.

I observed that cottonwoods in northern YNP consisted of two age-related growth forms: old trees, and younger densely-branched bushes (Figure 1). One objective of this study was to document the height-growth of bushes. A second objective was to determine if the height of browsing corresponded with winter snow depth. A third objective was to determine if there had been an

Figure 1. A young cottonwood near Soda Butte Creek, Yellowstone National Park. Bite marks indicate that the bush-form habit was produced by herbivory. Virtually all young cottonwoods in the northern elk winter range are restricted to a bush-form growth habit.

increase in the herbivory of cottonwood since the end of the elk reduction program in 1968. Evidence consistent with an increase in herbivory would be: 1) if younger bushes were browsed closer to the ground compared to older bushes, and 2) if there was not a corresponding decline in snow depth.

Methods

The study was conducted in northeast YNP on Soda Butte Creek 5.5 km upstream from its confluence with the Lamar River (elev. 2050 m). The average precipitation at Mammoth, WY is 412 mm. Substrates consisted of a poorly sorted alluvium with coarse clasts ranging from pebble-to-cobble in size.

Cottonwood bushes are presently uncommon in northern Yellowstone, so I designed a study to minimize coring and sectioning. The study was based on a comparison of stands of different age, thus reducing the need for the age determination of individual plants.

Five stands were assigned relative ages using aerial photographs. Stand 1 was visible on a 1954 photograph and was the oldest known stand of bushes in the area. Stand 2 was visible on a 1972 photograph, but not on the 1954 photograph. Stand 3 was first visible on a 1987 photograph. Stands 4 and 5 were not visible on the 1987 photograph.

I supplemented the relative ages indicated by photography with the dendrochronologic ages of plants presumed to be early colonizers of their respective stands. No plants in stand 1 were sectioned because all were dead and establishment date could not be fixed. Live, large plants were very rare in stand 2 and none were sampled. Relatively few large plants survived in stand 3 where 4 were sectioned. Twenty plants from each of stands 4 and 5 were sectioned. The bases of several plants from each stand were examined to determine if plants were established from seed or from root suckering.

Stand boundaries were defined so that plant height and density were approximately homogeneous within respective stands. Within each stand, 3 belt transects were placed at distance intervals along a baseline. Transects in stands 1 - 4 measured 2 x 25 m. Transects in stand 5 measured 1 x 10 m (plant density was about 5 times that of other stands).

Measurements were made in the summer of 1994. For each bush I recorded: 1) whether the bush was alive or dead, 2) the maximum height above ground level of live previous-year-growth, 3) whether or not that stem had been browsed, and 4) the height of the oldest browse-killed stem. Previous-year-growth was measured because it had experienced browsing during the winter of 1993-1994 while current-year-growth had not yet been browsed.

Browse-kill was defined to occur when at least 3 terminal twigs were dead, at least 1 of which was pruned by browsing. Within a bush, mortality may occur on a succession of shoots. The oldest such shoot was identified by: 1) a central position of the dead stem among a cluster of stems, and 2) condition of bark. A stem where bark was absent was interpreted to be older than a stem with frayed bark.

Transect data were pooled for statistical analysis. The variance of previous-year-growth height was homogeneous after natural log transformation and stands were compared by oneway ANOVA. Tukey's honest significant difference for unequal sample size, protected by a significant F-test, was used to test for differences between means. Variance of browse-killed stem height remained heterogeneous following natural log transformation (Hartley F-max = 2.9, $P < 0.001$). Stands were compared by Kruskal-Wallis ANOVA using natural log transformed data. Tukey's honest significant difference for unequal sample size, protected by a significant H-test, was used to test for differences between means.

Snow depth at January 1, January 15, February 1, and February 15 was used to calculate a mid-winter average snow depth for years of record. Data from 1950–1994 were from the Tower Ranger Station located 23 km west at 1,910 m elevation. Trends in snow depth thickness were tested by regressing average mid-winter snow depth *on* year. On 8 March 1995 I took 10 snow depth readings at the study site to compare with the snow depth occurring at the Tower Ranger Station.

Results

Based on the age of the oldest plants, stands 3, 4, and 5 were estimated to have been respectively created in 1968, 1977, and 1985. Using a combination of dendrochronology and photography,

stands 1–5 were inferred to be in sequence of decreasing age.

Stands 2 and 3 contained individuals that were established within a period ranging from respective stand creation to 1994. Recruitment in recent years was from root suckering. Stands 4 and 5 contained individuals established over the period from respective stand creation to 1991. Recruitment was from seed. The extent of root suckering in stand 1 could not be determined due to decay of the root system. The stems of many plants in all stands were decumbent.

Mean height of live previous-year-growth ranged from 12 to 33 cm tall (Table 1). The maximum height was 80 cm. All stems taller than 29 cm had been browsed. Mortality ranged from 100 % in stand 1 to 4 % in stands 4 and 5 (Table 1).

The mean height of the oldest browse-killed stems ranged from 9 to 87 cm tall (Table 1). Height was greater in older stands compared to younger stands (Kruskal-Wallis H = 358, $P < 0.001$). The untransformed variance was greater in older stands compared to younger stands (stands 1 - 5 respectively: 745, 399, 291, 21, and 15 cm^2).

Over the period 1950–1994, there was no long-term trend in the average mid-winter snow depth at the Tower Ranger Station (Y = 89.3 - 0.02 * X; the standard error of the regression coefficient was ± 0.16, $P = 0.89$, N = 45, Figure 2). On March 8, 1995 the snow depth at the Tower Ranger Station was 71 cm, 18 cm of which was new snow. On the same date, snow depth at the study site averaged 71 ± 0.7 cm (± SE; n = 10), 18 cm of which was new snow, with no evidence of disturbance to the snow surface.

Discussion

Narrowleaf cottonwood is capable of vigorous growth and in areas just outside of YNP, often attains more than 2-m height within a few years (pers. obs.). In contrast, the age of bushes in this study area represent a period of at least 45 years, yet the tallest live previous-year-growth was only 80 cm. The ubiquitous browsing of stems taller than 29 cm suggests that the bush growth-form has been maintained by intense herbivory. The survival of live stems to 80-cm-tall appears to result from the mechanical protection provided by thatches of browse-killed stems.

The average height of browse-killed stems measured in older stands was greater compared to the heights measured in younger stands. If a change in snow depth caused plants in younger stands to be browsed closer to the ground (compared to older stands), one would expect a corresponding decline in snow depth in recent time. There was no long-term decline in snow depth, indicating that this factor was not the cause of the change in the height at which plants were browsed.

Stands 4 and 5 appear to have experienced intense herbivory since establishment. The average height at which stems were killed by browsing was 14 and 9 cm respectively. Seventeen years after the creation of stand 4, the tallest live previous-year-growth was only 42 cm. The 17-year period

TABLE 1. Mortality, height of oldest browse-killed stems, and height of previous-year-growth.

	Stands in sequence of older to younger				
	1	2	3	4	5
Mortality (%)	100	82	10	4	4
Live previous-years-growth					
N	0	6	143	199	180
Mean height (cm) ± SE	—	$28^{ab} \pm 1$	$33^{a} \pm 1$	$18^{b} \pm 1$	$12^{c} \pm 1$
Maximum height (cm)	—	47	80	42	33
Tallest unbrowsed height (cm)	—	0[2]	29	24	22
Oldest browse-killed stem					
N	64	52	139	163	70
Mean height (cm) ± SE	$87^{a} \pm 1$	$62^{b} \pm 1$	$28^{c} \pm 1$	$14^{d} \pm 1$	$9^{e} \pm 1$
Maximum height (cm)	173	101	85	30	22

[1] Similar superscript letters denote means which did not differ at $P < 0.001$.

[2] All stems were browsed.

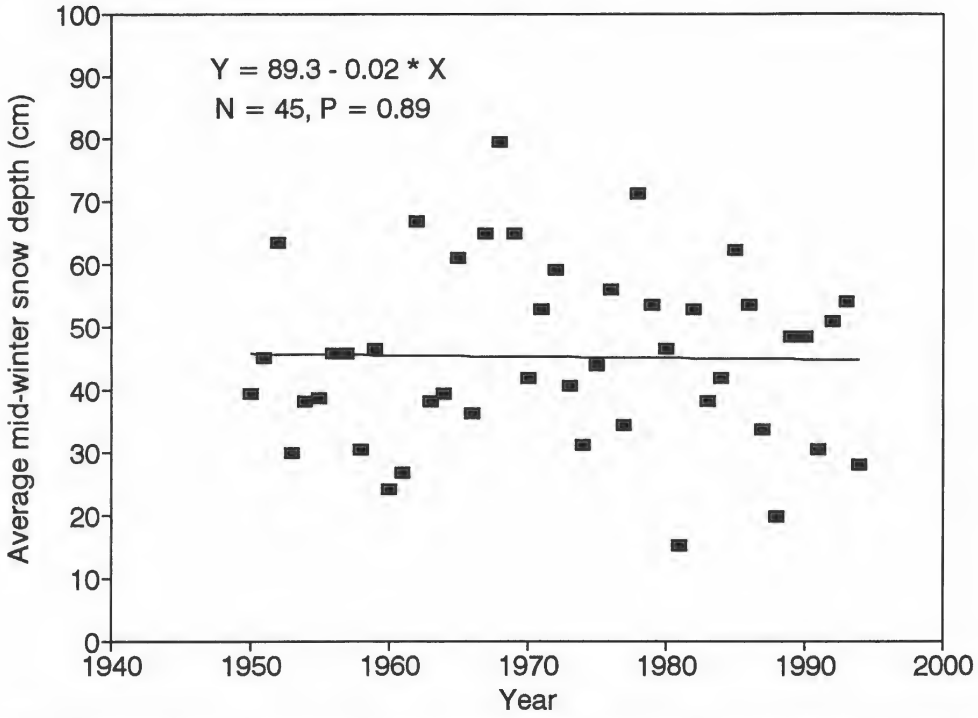

Figure 2. Snow depth can influence the height at which cottonwoods are browsed. Average mid-winter snow depth from 1950-1994 was examined to determine if a recent decrease in snow depth could have caused younger plants to be browsed more closely to the ground compared to older plants. Over that period there was no significant change in the average mid-winter snow depth.

of intense herbivory experienced by stand 4 provides an opportunity to explore the relationship between snow depth and season of browse use.

The average mid-winter snow depth for the period since establishment of the stand (1977–1994) was 43 cm. If height of browsing is controlled by mid-winter snow depth, the variance of the height at which stems are killed by browsing should be similar to the variance in mid-winter snow depth. The variances of browse-killed stem height and average mid-winter snow depth were 21 and 199 cm^2, respectively. A Hartley F-max ratio of 9.8 ($P < 0.001$) indicates that the height of browsing is significantly more uniform than mid-winter snow depth.

Two lines of evidence suggest that herbivory occurs when snow is less deep than the mid-winter level. First, on average plants in stand 4 were browsed at 14 cm, ca. 30 cm below the mid-winter snow depth of 43 cm. Second, the height of browsing does not reflect annual variation in snow depth, thus indicating that elk did not consistently remove 30 cm of snow to reach the buried plants. During autumn, snowcover becomes partially responsible for the increased use of browse relative to forbs and grass (Nelson and Leege 1982). The height at which stems were cropped in stand 4 (and stand 5) may record a snow depth at which browse becomes important in the elk diet.

Before browsing killed the tips of stems in stands 1, 2, and 3, those stems grew taller than the stems measured in stands 4 and 5. A stem in stand 1 grew to 1.7 m tall. Growth to this taller height suggests an early period of less intense herbivory compared to the present. A prior period of less intense herbivory would be consistent with the reduced elk population that was present during the late-1960's.

Herbivory would consistently inhibit the height growth of plants in a stand established after an

increase herbivory. In contrast, a stand established prior to an increase in herbivory would logically contain: 1) individuals established prior to the increase (the initial height growth of which would not have been limited by browsing), and 2) individuals established after the increase (the height growth of which would have been limited by browsing). Compared to the first stand described above, there would be greater variation in browse-killed stem-height in the second stand.

Pairwise comparisons of browse-killed stem-height variances suggest that herbivory increased between the creation of stand 3 in 1968 and stand 4 in 1977 (Figure 3). Chronic pruning since stand creation is inferred to have produced the relatively low variances of stands 4 and 5 (21 and 15 cm^2, respectively). The relatively large variance (i.e., compared to stands 4 and 5) of stand 3 (291 cm^2) is inferred to have been produced when the growth of plants that had attained a variety of heights (approximately corresponding to each of their ages) was halted by an increase in herbivory. Plants in stand 3 that were established subsequent to the increase in herbivory would be cropped close to the ground.

Where recruitment is continuous, older stands contain a wider range of ages compared to younger stands. For this reason, significant differences in stem-height variance such as that found in the comparison of stands 1 and 2 are to be expected.

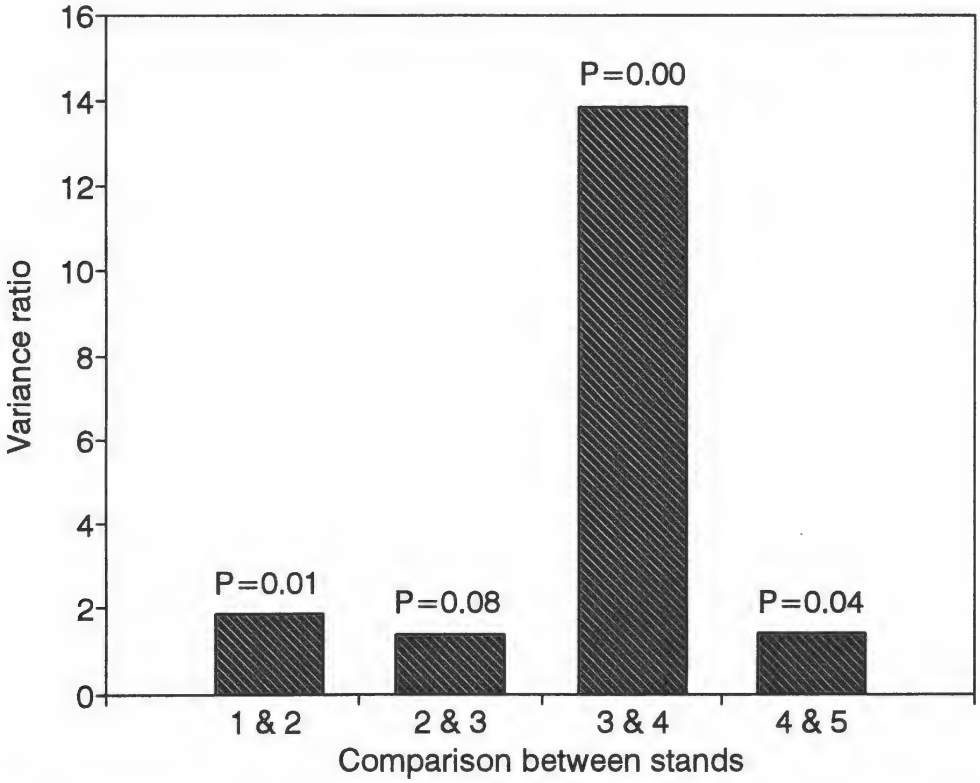

Figure 3. The cottonwood stands were mixed-aged due to continued recruitment after stand creation. Stands established prior to an increase in herbivory would contain cottonwoods whose height growth was not limited by herbivory, and cottonwoods whose height growth was limited by herbivory. Herbivory would kill stem tips at diverse heights above ground level. Plants in stands established after an increase in herbivory would be browsed at a more-uniform height. In sequence of decreasing stand age, pairs of variances of browse-killed stem height were compared by ratio test. The seven-fold difference between the variance ratio of stands 3 and 4 and the ratio of other variance pairs is distinct in magnitude. The ages of those stands mark a period within which browsing intensity increased.

It is the magnitude of difference that suggests that the comparison of stem-height variances of stands 3 and 4 is distinct from the other paired comparisons.

The increase in browsing intensity appears to have occurred some time between the creation of stands 3 and 4 (1968–1977). Over this period, the number of elk counted during the winter census increased from 3,172 to 8,981 (Houston 1982; Figure 4). I hypothesize that the increase in cottonwood herbivory was caused by an increase in the northern elk herd.

The pre-1968 period of less-intense herbivory may have been brief. Plants in stand 1 have decumbant stems that are similar in form to the stems found on young cottonwoods that are currently intensely browsed. In autumn 1961, the northern elk herd was estimated to number 10,000 (Howe, unpublished YNP report). During the 1961–1962 elk reduction, 5,135 animals were culled from the herd. It is plausible that a herd reduction of this magnitude could have a significant effect on herbivory. I hypothesize that plants in stand 1 experienced: 1) intense herbivory from ca. 1950 (i.e., since establishment) to 1961, 2) a reduction in herbivory beginning in 1962, and 3) an increase in herbivory sometime between 1968-1977. The decumbent stems observed in stand 1 could have been produced during that initial period of intense herbivory.

The reduction in herbivory hypothesized to have begun in 1962 only permitted growth to 1.7 m tall. If the period of less-intense herbivory spanned on the order of 10 years, this height is short compared to the potential 10-year-growth of young cottonwood. Height growth during that period may have been limited by stress due to herbivory prior to 1962, moderate herbivory from

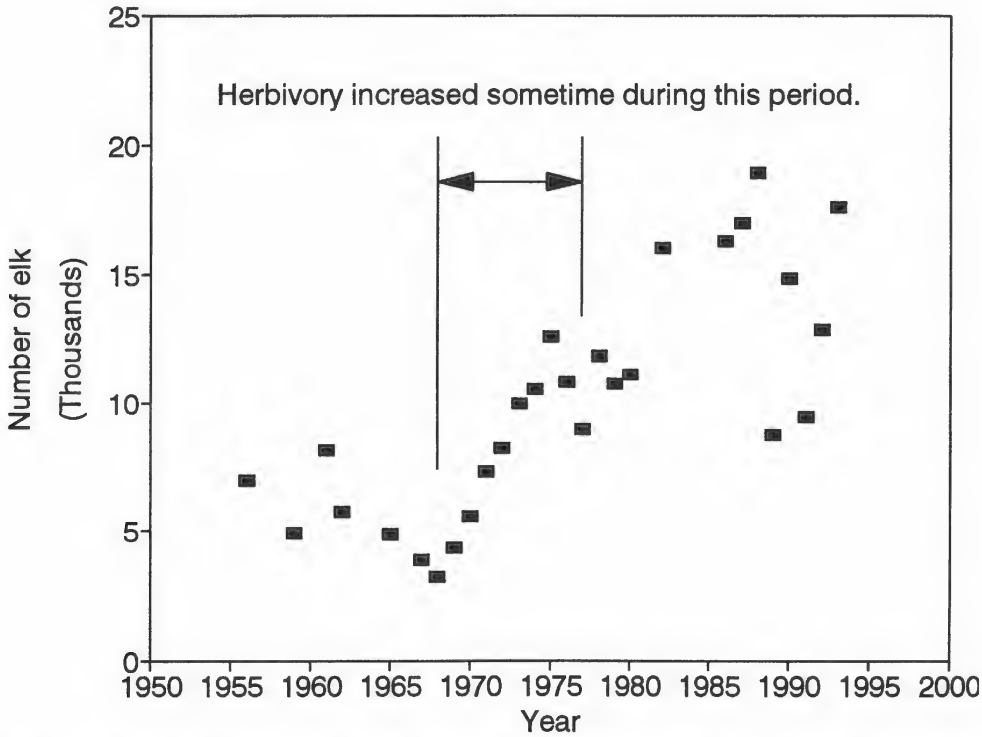

Figure 4. Browsing was inferred to have become intense some time within the period 1968-1977. During this period the elk population increased from a winter census of 3,172 to 8,981. Data are from Houston (1982) and Coughenour and Singer (1996).

1962 until the increase in 1968–1977, or unfavorable site conditions.

Mortality in stands 1 and 2 (respectively, 100 and 82%) was greater than the 4% measured in stands 4 and 5. The difference in mortality may reflect the number of young, latent buds protected by snowcover. The chronic cropping of young plants may increase the number of buds that are produced close to the ground. As the tips of stems are browsed, replacement branches can develop from the activation of latent buds. Plants in stands 4 and 5 may owe their high rate of survival to chronic intense herbivory that has occurred since establishment.

Compared to stands 4 and 5, plants in stands 1 and 2 may have experienced a period of rapid elongation, thus producing fewer buds close to the ground. If the plants were topkilled by an increase in herbivory, there may have been few young, latent buds protected by snowcover from which to replace the browse-killed stems. Plants that rapidly attain 1-to-2-m height may be especially vulnerable to a subsequent increase in herbivory.

Although plants in stands 4 and 5 appear to tolerate chronic intense herbivory, it is uncertain whether the cottonwood population can be maintained. Recruitment in stands 4 and 5 was from seed. Because the bushes do not produce seed (pers. obs.), continued recruitment depends on the survival of older seed-producing trees. As the surrounding trees die, the local cottonwood population may significantly decline. Elsewhere on the northern range I have not observed cottonwood bushes to grow as vigorously as they do in the vicinity of Soda Butte Creek. The cottonwood stands in the Soda Butte Creek area likely represent a best-case scenario with respect to cottonwood regeneration on the northern range.

Throughout much of this century, intense herbivory in YNP has been attributed to an overpopulation of elk caused by EuroAmerican influences (Graves and Nelson 1919, Wright and Thompson 1935, Kay 1990). Keigley and Wagner (ms in review) estimate the pre-YNP northern elk herd numbered ca. 5,000– 6,000 and that the herd was more migratory compared to the present. In the winter elk migrate from high elevations in YNP to lower, less-snowcovered elevations. Prior to the establishment of YNP, elk were reported to use an ancestral winter range north of YNP (Graves and Nelson 1919). Elk use of that range was inhibited when it was settled in the late 1800s. After the establishment of YNP, hunters concentrated just outside the park border. Hunting at the YNP border has been found to cause an artificial concentration of elk in the park through conditioned avoidance behavior (Houston 1979). Predation was essentially eliminated by the extirpation of the wolf (*Canis lupus*) and protection from human hunters. In combination, these factors would cause an increase in the number of elk using the present winter range.

In the past 25 years, two additional explanations have been proposed. Houston (1982, p. 136) and Despain et al. (1986, p. 104) attributed the declines of aspen to be primarily because of past fire suppression by the NPS. Houston was of the opinion that, "The effects of fire suppression may be largely reversible as fires are again permitted to burn." In 1988 YNP experienced widespread fire. Romme et al. (1995) found that elk continued to prohibit the growth of aspen to tree stature in burned areas.

Singer et al. (1994) speculated that "...a more xeric climate, lowered water tables, and/or changes in hydrological patterns contributed to the willow declines and changes in chemistry production on the northern winter range." Their principal evidence was the observation that heavily-browsed willows contained lower levels of chemical defense compounds compared to less-heavily-browsed plants. By this scenario, the environmental factors listed above caused a reduction in chemical defenses that then attracted increased elk use.

In a response to Singer et al. (1994), Wagner et al. (1995) pointed out that reduced levels of chemical defenses can be a *result*—as well as a *cause*—of intense herbivory. The data presented by Singer et al. support this interpretation. In their study, Singer et al. found that heavily browsed willows outside of an exclosure produced significantly less condensed tannin than did protected willows inside the exclosure. Because the environment inside and outside the exclosure is similar except for herbivory, this relationship suggests that the reduced chemical defenses are a *result* of herbivory. In response to Wagner et al. (1995), Singer and Cates (1995) presented the case that a "complex, multi-causal situation, where interactions between elk abundance, climate change, fire,

mammalian predators, and beaver abundance, might all influence the status and recruitment of willows." No specific model was described.

The fire suppression and environmental change theories (i.e., Houston 1982, Singer et al. 1994) were based primarily on the physiology and ecology of aspen and willow, respectively. A more realistic assessment of probable cause should begin with a complete description of the browse species that are in decline as a result of elk use. In my opinion, that list would include most of the woody plants on the northern range. If a broad spectrum of species is confirmed to be intensely browsed, it may become difficult to support the theories above. For example, it is questionable whether the degree of environmental change observed in YNP would reduce the vigor or production of chemical defenses of all members of such a physiologically-diverse group of plants.

The episodic nature of disturbance may make it impossible to define the natural vegetation or the natural disturbance regime in many areas (Sprugel 1991). Could the intense herbivory in YNP be part of a natural—but infrequent—cycle? If the present intense herbivory is to be generally accepted as a natural circumstance, it will be necessary to identify the natural processes responsible. To date, this has not been accomplished. On the other hand, the potential effect of predator elimination is well understood: prey populations may increase. And as a matter of practice, game management agencies take into account the possibility that elk migratory behavior can be altered by a variety of human influences. At the present time, the weight of evidence appears to favor the explanation that EuroAmerican influences are responsible for the decline of cottonwood and other browse species in northern YNP.

Acknowledgements

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Effects of Prescribed Burning on the Viability of *Armillaria ostoyae* in Mixed-Conifer Forest Soils in the Blue Mountains of Oregon

Abstract

This study evaluated the influence of prescribed burning, soil depth, antagonistic fungi (*Trichoderma harzianum* Rifai), and time since burning on the viability of the root pathogen *Armillaria ostoyae* (Romagnesi) Herink in wood pieces buried in the soil of a mixed-conifer forest in northeastern Oregon. Red alder (*Alnus rubra* Bong) stem segments colonized with *A. ostoyae* were buried at two soil depths in plots that were burned and not burned. Half of the *Armillaria* segments were buried with segments of *T. harzianum*. Prescribed burning in the fall significantly reduced the recovery of *A. ostoyae* immediately after the burn at a soil depth of 8 cm but not at a soil depth of 30 cm. Adding *T. harzianum* inoculum to the soil did not appear to reduce *A. ostoyae* recovery immediately after the fire, but effects appeared after several months. Differences may also be due to the timing (fall or spring) of the prescribed burns. The effects of fire either natural or prescribed on pathogenic and saprophytic fungi may greatly influence infections of woody roots, subsequent disease occurrence, and patterns of tree mortality.

Introduction

Fire has been a component of the natural environment for 350 million years (Agee 1993). In the upper elevation, mixed-conifer forests of northeastern Oregon, fire return intervals have historically ranged between 40-150 years (Mutch et al. 1993). Because of these fire patterns, stands had a dominant overstory of ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) with scattered large-diameter western larch (*Larix occidentalis* Nutt.), Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco), and grand fir (*Abies grandis* (Dougl. ex D.Don) Lindl.). Large diameter trees were common, and insect and pathogen populations remained at endemic levels due to low stand densities and the mixed-species stands.

Fire exclusion and selective harvesting of pine and larch that began at the turn of this century have resulted in an unprecedented abundance of grand fir and Douglas-fir in many areas in the interior West (Filip 1994). Mortality from root disease and other pests is much greater in stands with more true firs (Filip and Goheen 1984, Filip et al. 1996). As a result, these stands are overstocked with diseased, suppressed, or dead grand fir, Douglas-fir, and ponderosa pine.

Prescribed burning is increasingly used throughout northeastern Oregon in an attempt to return fire to its natural role in the ecosystem. Only a few studies, however, have directly linked fire in the Pacific Northwest to the changes in the incidence or severity of root pathogens (Thies 1990). Understanding the effect of prescribed burning on root disease will help to elucidate the relationship between fire and root disease.

Several species of the fungus *Armillaria* cause a serious root disease in host plants (Shaw and Kile 1991). Until the late 1970s it was assumed that Armillaria root disease was caused by a single polymorphic species, *A. mellea* (Vahl. ex Fr.) Kummer. Several species within the genus are now recognized (Kile et al. 1993). In North America, nine species have been defined; *A. ostoyae* is the most pathogenic species for conifers (Gregory et al. 1991). In the mixed-conifer forests of northeastern Oregon, *A. ostoyae* is common and widely distributed (Schmitt et al. 1991). Schmitt found that grand fir had the highest incidence of damage from several species of root pathogens, that ponderosa pine was damaged more by *A. ostoyae* than other root pathogens, and that Douglas-fir was damaged by root pathogens in most sample strata and plant associations.

Armillaria ostoyae is a saprophytic and weak parasitic fungus that can become an aggressive tree-killing pathogen (Wargo and Shaw 1985, Shaw and Kile 1991). *Armillaria ostoyae* can survive in stumps and dead roots for at least 50 years as mycelia or rhizomorphs; they can infect adjacent living trees via mycelium across root grafts and contacts or through rhizomorphs. The black, shoestring-like rhizomorph is an important infective structure that allows the fungus to colonize large

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areas. The fungus attacks, colonizes, and kills apparently healthy trees of all ages, often creating canopy gaps or patches. It has proven difficult to eradicate the fungus from an infected site. At many sites, stump and root colonization has led to a substantial increase in the inoculum in the soil which contributes to the increased severity of root disease (Filip and Goheen 1984, Wargo and Shaw 1985, Shaw and Kile 1991).

Biological control of *Armillaria* spp., although promising *in vitro*, has been unsuccessful for the most part *in situ*. Species of *Trichoderma* are reported to be the principal invaders of wood colonized by *Phellinus weirii* (Murr.) Gilb., the cause of laminated root rot (Nelson 1982, Goldfarb et al. 1989). Yang and Hood (1992) reported that a species of *Trichoderma* was markedly antagonistic toward *A. novae-zelandiae* (Stevenson) Herink. and *A. limonea* (Stevenson) Boesewinkel on freshly cut radiata pine (*Pinus radiata* D. Don) segments as compared to its interaction with eight other common saprophytic fungi. Munnecke et al. (1981) showed that *Trichoderma* spp. were responsible for the death of *Armillaria* mycelia on citrus trees after *Armillaria* had been "stressed" by fumigation with carbon disulfide in California. Filip and Roth (1977) found a significant increase in *Trichoderma* spp. in ponderosa pine stumps treated with methyl bromide or vorlex as compared to untreated stumps in central Washington.

Biological control of *Armillaria* is difficult because effective populations of antagonistic fungi are not sustainable under normal field conditions. Because prescribed fire treatments can influence antagonistic soil microorganisms (Margaris 1977, Parmeter 1977), judicious use of fire may indirectly help minimize Armillaria root disease. In central Oregon, Reaves et al. (1984) found that ash leachates from prescribed burns in ponderosa pine forests reduced the growth of *A. ostoyae* in cultures. Isolates of *Trichoderma* spp. obtained from burned soils were more antagonistic to *A. ostoyae* in culture than isolates from unburned soils (Reaves et al. 1990).

The purpose of our study was to determine whether prescribed burning reduces the viability of *A. ostoyae* in wood segments buried in a mixed-conifer forest soil. We were specifically interested in four issues: (1) whether there is a significant difference in the viability of *A. ostoyae* inoculum segments between burned and unburned treatments; (2) whether the treatment difference is associated with the depth of buried segments (8 cm vs. 30 cm); (3) whether the treatment difference is associated with the presence of *Trichoderma harzianum*; and (4) whether the treatment difference is associated with time since the prescribed burning treatment (over a year).

Methods

Research Site

The study was conducted in the Genesis Demonstration Area (T12S, R34E, Sec. 23; T13S, R34E, Sec. 1) in the Prairie City Ranger District, Malheur National Forest of Oregon. Four plant associations occur in the research area: *Abies grandis/Calamagrostis rubescens*, *A. grandis/Carex geyeri*, *A. grandis/Vaccinium membranaceum*, and *A. grandis/V. scoparium* (Johnson and Hall 1990). Stands in the study area contained dying and dead grand fir and Douglas-fir due to an outbreak of western spruce budworm (*Choristoneura occidentalis* Freeman) from 1980 to 1992.

Stands in the research area were part of a timber sale during the late 1970s and early 1980s. The most recent sales included regeneration harvests in mixed-conifer stands, overstory removals, and precommercial thinnings in ponderosa pine and fir stands. Harvesting, which began in 1978, fell victim to the timber buy-back program of the early 1980s and was not completed until 1991 after timber resale in 1987.

Three units in the study area were selected because of their prescribed fire treatment priority. Units A and B were selectively harvested in order to reduce excess stand density and favor ponderosa pine and western larch. Unit H was clearcut. Prescribed fire was planned in all three units in order to reduce fuel loads and create planting spots.

Fungal Inoculation

Because of the uneven distribution of Armillaria root disease in the study area, an isolate of *Armillaria ostoyae* from northeastern Oregon was used to artificially inoculate the treatment blocks. *Trichoderma* spp. were isolated from the soil at the research sites. A preliminary laboratory test was performed in order to screen for the *Trichoderma* isolate that was the most antagonistic to *A. ostoyae*; an isolate of *T. harzianum* was used as the inoculum.

Red alder (*Alnus rubra* Bong.) stem segments were obtained in the Oregon Coast Mountains. Segments were approximately 12 cm x 2.5 cm (with bark) and were soaked overnight in tap water; 4-6 were placed vertically into glass jars. Jars were 1/4 filled with water and autoclaved at 120°C for one hour. The segments were cooled overnight and inoculated with *A. ostoyae* grown on 3% malt agar. Jars were incubated in the dark at (18-24°C) for 3 months until the segments were well colonized by *A. ostoyae*. *Trichoderma-harzianum*-inoculum segments were similarly prepared from autoclaved red alder stem segments, but were incubated for one month.

Experimental Design and Plot Establishment

Two blocks each were randomly established in units A, B, and H in the study area: blocks 1 and 2 in unit A, blocks 3 and 4 in unit B, and blocks 5 and 6 in unit H. Each block was designed with a split-plot configuration. The use of prescribed burning was the whole-plot factor, and soil depth and presence of *Trichoderma* were the sub-plots factors. Each 12 m x 24 m sub-block (burned or unburned) contained four plots (Figure 1). Treatments were randomly assigned to the plots. Fifteen red alder stem segments colonized with *Armillaria* were buried in each plot before burning; five segments were buried for each of three sampling times (1 day, 1 month, and 2 months after burning). A *Trichoderma*-inoculum segment was buried adjacent to and touching an *Armillaria*-inoculum segment where indicated (AT). An iron stake was placed at each corner and at the center of each plot. The position of each inoculum segment was measured from the closest iron stake and recorded on a map for future sampling.

The configuration was a 2^3 factorial design; the treatments were burned or unburned, 8 or 30 cm soil depth, and presence or absence of *Trichoderma* inoculum. All segments were randomly assigned to each treatment and buried between August and September 1993. Before the prescribed fire treatment, woody debris was evenly scattered over each plot so that burning was uniform.

Prescribed Burning

Unfortunately, local weather and the availability of personnel at the Prairie City Ranger District affected our ability to field burn. Instead of burning all six blocks in the fall of 1993 as planned, the fire treatment occurred at three different times over two years.

Blocks 5 and 6 in H unit were burned for an hour on 27 October 1993 (Figure 2). The woody debris and litter layer on both blocks was barely consumed; soils were moist to the touch. On 31 October 1993, the burned plot of block 6 was reburned for four hours; the first sampling of segments occurred the next day, the second sampling occurred in June 1994, and the third in August 1994.

Block 3 in unit B and block 5 in unit H were burned on 8 June 1994, nine months after inoculation. The fire which lasted one hour and was extinguished with water, completely consumed the woody debris and litter layer (Figure 3). We began sampling the next day, sampled a second time in July, and a third time in August.

Blocks 1, 2, and 4 in units A and B were burned on 27 October 1994, one year after inoculation. The fire lasted one hour and completely consumed the woody debris and litter layer. Water was used on all plots to extinguish the fire. Sampling for Blocks 1, 2, and 4 was done only on the day after the burn. These 3 blocks received the same treatment, so data could be statistically analyzed.

Inoculum Recovery

Following each prescribed fire treatment, five segments from each treatment were randomly selected in order to test the viability of *A. ostoyae* at each sampling time. Segments were excavated individually, bagged in separate paper bags for each treatment, and stored at 1-2°C until they were processed in the laboratory. We attempted to isolate the fungi by splitting each segment aseptically and plating five wood chips (1 x 1 x 1 mm) onto a selective medium for *Armillaria* (2% malt agar with 1.5 ppm each of prochloraz, benomyl, and thiabendazole; 30 ppm rose bengal; and 100 ppm streptomycin sulfate; Goldfarb et al. 1989). The recovery rate of *A. ostoyae* was scored from 0-5 based on the number of isolates recovered from that segment. The number of *A. ostoyae* isolates recovered was converted to 0-100% scale. Treatment means were the average of the 15 segments in that treatment.

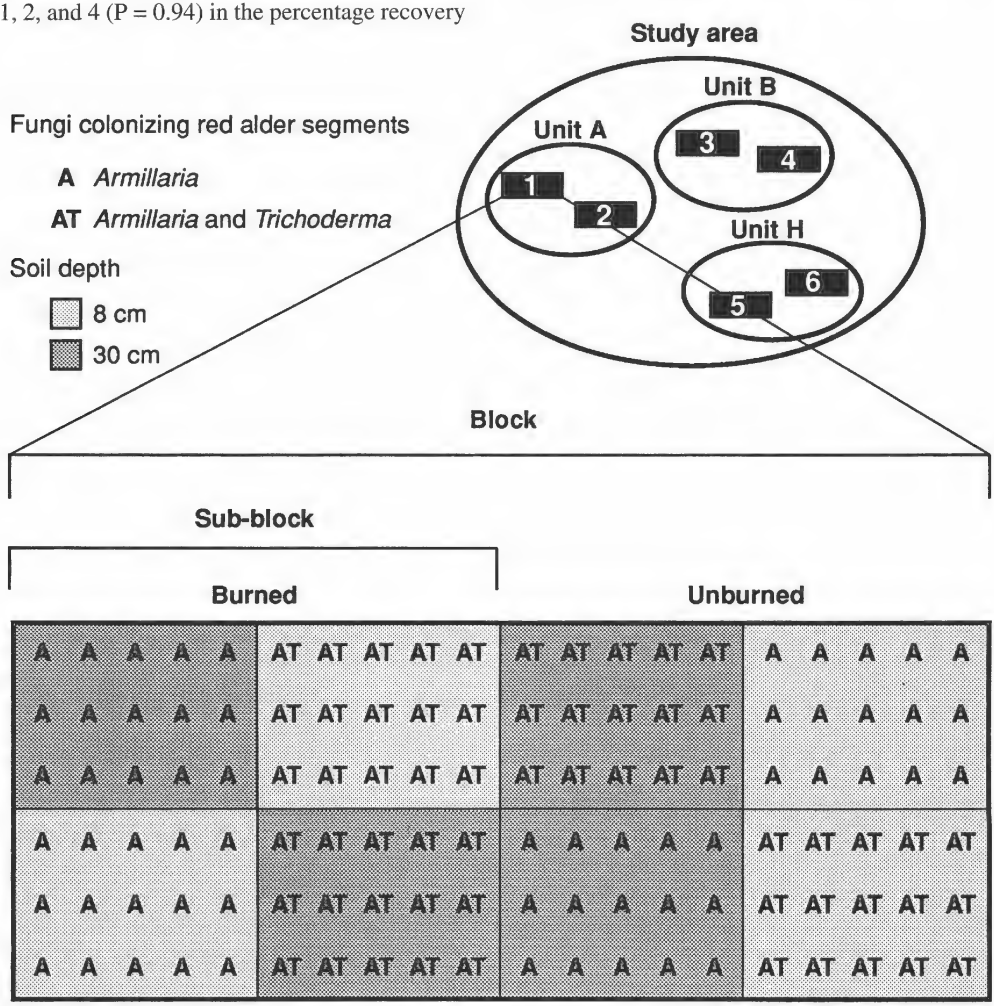
Statistical Analysis

Percent recovery of *A. ostoyae* was tabulated by burning treatment, soil depth, and presence of *Trichoderma*. Data from blocks 1, 2, and 4 were

examined by using analysis of variance for a 2^3 factorial with an F test ($P<0.05$; SAS Institute, Inc. 1994). We explored the main and interactive effects of prescribed burning, depth of inoculum, and the presence of *Trichoderma* on the percentage recovery of *A. ostoyae*. Comparisons were made between all combinations of treatments.

Results

There were no significant differences among blocks 1, 2, and 4 ($P = 0.94$) in the percentage recovery of *Armillaria* immediately after the prescribed burn in October 1994. The effect of prescribed burning on *Armillaria* viability was significant ($P = 0.0138$; Table 1). The interaction between the prescribed burn and soil depth on *Armillaria* viability was also significant ($P = 0.0138$). The 3-way interaction of prescribed burning, soil depth, and the presence of *Trichoderma* ($P = 0.3003$), the interaction between prescribed burning and the presence of *Trichoderma* ($P = 0.4313$), and


Study area
Unit B
Unit A
Unit H
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2
3
4
5
6
Fungi colonizing red alder segments
A Armillaria
AT Armillaria and Trichoderma
Soil depth
8 cm
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Figure 1. Diagram of the plot configurations and randomized treatment applications within each block. Red alder segments, colonized by *Armillaria* (A) were buried 8 or 30 cm under the soil surface (soil depth). In some cases, a segment colonized by *Armillaria* and a segment colonized by *Trichoderma* were buried together (AT). The plots in which these segments were buried were subsequently subjected to prescribed burning treatments.

Figure 2. Field crews igniting debris near plots used to determine effects on *Armillaria* viability.

Figure 3. Typical plot after burning and prior to sampling for *Armillaria* viability.

the interaction between soil depth and the presence of *Trichoderma* (P = 0.9193) did not significantly affect the viability of *Armillaria*.

Prescribed Burning and Soil Depth

The recovery of *Armillaria* decreased significantly from 36 to 5% at soil depths of 8 cm in burned plots but remained unchanged at soil depths of 30 cm (Table 2). The recovery of *Armillaria* was lowest in the burned and highest in the unburned treatments at a soil depth of 8 cm. The mean recovery of *Armillaria* at the 8 cm depth with prescribed burning was 5% which is not statistically different than 0% recovery (P = 0.43); thus *Armillaria* at a soil depth of 8 cm had virtually no viability after the prescribed burning). The mean recovery of *Armillaria* in unburned plots was 36% at 8 cm and 19% at 30 cm; however, depth itself did not have a significant effect on the percentage recovery of *Armillaria* in unburned plots (P = 0.8059; Table 1).

Season of Burning

Block 6 in Unit H was burned in the fall 1993 and sampled three times: fall 1993, spring 1994, and fall 1994. Because this was the only block effectively treated in fall 1993, there was no statistical analysis. In plots treated with prescribed burning, the recovery of *Armillaria* appeared to remain the same at the 30 cm soil depth regardless of the time of sampling; however, recovery decreased at the 8 cm depth at the second sampling. In unburned plots, the recovery of *Armillaria* at a depth of 8 cm was higher than at 30 cm at the second and third samplings.

TABLE 1. Results of an analysis of variance of the effects of prescribed burning (Burn), soil depth, and presence of *Trichoderma* (*Trich*) on the viability of *Armillaria* inoculum.

Source	NDF[1]	DDF[1]	Type III F[1]	Pr > F[1,2]
Burn	1	14	7.92	**0.0138**
Soil depth	1	14	0.06	0.8059
Trich	1	14	0.14	0.7181
Burn x Depth	1	14	7.92	**0.0138**
Burn x *Trich*	1	14	0.66	0.4313
Depth x *Trich*	1	14	0.01	0.9193
Burn x Depth x *Trich*	1	14	1.16	0.3003

[1]NDF = numerator degrees of freedom; DDF = denominator degrees of freedom; Type III F = Type III F-value; and Pr> F = probability greater than F-value.

[2]Bolded values are significant.

TABLE 2. The percentage recovery of *Armillaria ostoyae*, in northeastern Oregon, at two soil depths and at burned and unburned sites.

Treatment	Soil depth (cm)	Mean[1]	SE
Burned	8	5 (0.23)a[2]	0.29
Burned	30	19 (0.95)ab	0.29
Unburned	8	36 (1.83)b	0.29
Unburned	30	19 (0.95)ab	0.29

[1] Means are the percentage and actual number (in parentheses) of viable isolations of *A. ostoyae* out of a total of five attempts from each of 15 segments per treatment.

[2] Means followed by a different letter are significantly (P<0.05) different according to ANOVA (SAS Institute, Inc. 1994).

Following the burning treatment, the recovery of *Armillaria* appeared to decrease with time in the presence of *Trichoderma* but increased in the absence of *Trichoderma*. Without the burning treatment, recovery of *Armillaria* increased at the second sampling, then decreased at the third sampling, especially in the presence of *Trichoderma*.

Block 3 in Unit B was burned in spring 1994 and sampled three times: June, July, and August 1994. Block 5 in Unit H was also burned in the spring, but the unburned plot was accidently destroyed. The spring burn seemed to have no effect on the recovery of *Armillaria* during the sampling period. At the second and third sampling, *Armillaria* recovery in burned plots at the 8 cm depth was higher than recovery at 30 cm. The presence or absence of *Trichoderma* appeared to have little affect on *Armillaria* recovery.

Discussion and Conclusions

There was a significant reduction in *Armillaria* recovery immediately following a fall burn. The recovery of *Armillaria* was lowest (5%) in burned plots and highest (36%) in unburned plots in segments at a soil depth of 8 cm. The results of this field study suggest that the heat from the fire was able to kill a high proportion of *Armillaria* at a soil depth of 8 cm but not at 30 cm. The fact that most segments were scorched by the fire in all three blocks further supported the conclusion that the reduction in *Armillaria* recovery was caused by heat. Hood and Sandberg (1989) reported that

there was a highly significant reduction in the yield from isolates of rhizomorphs, although no significant change in rhizomorph frequency, after felling and burning of forest vegetation in New Zealand.

Trichoderma harzianum can kill *Armillaria* mycelium in agar media in laboratory tests. The shift in the microbial balance from ash leachates in forest soils (Reaves et al. 1990) that favors the antagonist *Trichoderma* following a prescribed fire is a rather slow process compared to lab tests. We did not find a decrease in *Armillaria* with *Trichoderma* in samples taken immediately after the fire, although 8-10 months after the prescribed burning we found a decrease in *Armillaria* recovery. Additional research is needed in order to evaluate whether the reduction in *Armillaria* recovery is short-term. Also, there are large natural populations of *Trichoderma* spp. in forest soils that we did not monitor.

There was no apparent difference in the recovery of *Armillaria* between burned and unburned plots after the spring burning treatment. This differs from the results after the fall burning; we found a significant difference between burned and unburned plots at the 8 cm soil depth. More studies are needed to establish the timing and intensity of fire that are necessary to effectively reduce *Armillaria* recovery.

Prescribed burns should have occurred in all blocks in fall 1993. Instead, prescribed burning occurred at three different times over two years. Use of prescribed burning on public land involves a systematic series of decisions. The steps in this process include examining the proposed burn unit, developing prescriptions, obtaining permits and resources, addressing public concerns, checking weather and fuel conditions, selecting ignition patterns and tools, conducting the burns, and mopping up after completion.

Waiting for suitable weather conditions is a primary constraint in prescribed burning. Both the fuel and atmospheric conditions must be dry enough to support combustion, yet not so dry that escape of the fire is likely. This creates very narrow windows for treatment given the spring snow cover, dry and hot summers, and rainy autumns in eastern Oregon.

Woody roots that are naturally infected with *Armillaria* are normally present at depths much greater than were inoculum segments in our study. Obviously, an operational burn with conditions similar to our study would only destroy a small portion of the total *Armillaria* inoculum. Unless the burn was hotter or more penetrating, a situation that could lead to soil damage and significant nutrient loss, the direct effects of prescribed fire on *Armillaria* populations appear to be negligible. The long-term effect of burning as related to changes in *Trichoderma* populations and subsequent indirect effects on *Armillaria,* however, may be more important. Except for Reaves et al. 1984, 1990, and our study there are no studies on fire and root disease in interior western forest ecosystems. Long-term studies that explore the effects of prescribed burning on naturally infected roots in soil need to be conducted.

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Vertical Profile of Epiphytes in a Pacific Northwest Old-growth Forest

Abstract

The vertical stratification of epiphytes is a striking feature of Northwestern forests that surely influences the distribution of other organisms in the canopy. We are just now learning how and why the stratification varies from place to place. Functional groups of epiphytes were stratified with height in an old-growth *Pseudotsuga-Tsuga* forest in the following order, from the ground up: bryophytes, cyanolichens, and alectorioid lichens. Other macrolichens (mainly green-algal foliose) were found throughout the vertical profile, but their relative abundance peaked in the middle to upper canopy. Cyanolichens (mainly *Lobaria oregana*) were concentrated in the "light transition zone." The light transition zone is the range of heights in which we found abrupt transitions in light transmittance by the canopy. This zone extends from about 13 to 37 m in height, in an overall canopy height of 50-60 m. Bryophytes were concentrated between the ground and the middle of the light transition zone. The biomass of epiphytic macrolichens was about 1.3 metric tons/ha, composed of approximately 42% cyanolichens, 28% alectorioid lichens, and 30% other lichens.

We draw the following methodological conclusions. Using quadrats as windows from a suspended gondola overestimates the relative abundance of alectorioid lichens and underestimates cyanolichens and other lichens. Using 14, 2-m radius lichen litter plots is barely adequate to represent the epiphytic macrolichens of an old-growth stand. Ground-based canopy density measurements (photographic and densiometer) are insufficient to characterize the openness of a vertical transect, because of interference from understory vegetation.

Introduction

Communities of canopy epiphytes change conspicuously with height in the conifer forests of the Pacific Northwest (Pike et al. 1975, McCune 1993, Sillett 1995). The sequence of dominance with increasing height is fairly constant in different areas of the Pacific Northwest. Bryophytes dominate near the ground, then cyanolichens, alectorioid lichens, and other macrolichens (mainly green algal foliose lichens) dominate progressively higher zones in the canopy. The depth of these zones varies with climate and forest age. McCune (1993) hypothesized that the zones shift upward in wetter climates or as forests age, but that the basic sequence of dominance remains the same. So few stands have been profiled, however, that this hypothesis remains unsubstantiated.

The goal of this study was to characterize the profile at a new site and to compare the vertical profile of epiphytes with the vertical profile in light transmittance. Would the vertical profile of epiphytes shift downward in more open parts of the canopy?

The canopy crane at the Wind River Experimental Forest provided us with an opportunity to meet these objectives. Studying the forest from a suspended gondola created a need for a new method for non-destructive sampling of the vertical profile in epiphyte communities, subject to a constraint that we would often be beyond reach of the substrates we were sampling. We also collected lichen litter data to estimate the absolute and relative abundance of three functional groups of epiphytic lichens. These litter data allowed estimates of canopy lichen biomass and provided an independent check on data quality from the sampling via the gondola.

Study Area

We studied the forest of the Wind River Canopy Crane Research Facility in the southern Washington Cascades. The canopy crane is a large construction crane on a fixed platform, providing 3-dimensional access to a 2.3 hectare circular area of old-growth *Pseudotsuga menziesii - Tsuga heterophylla* forest (Franklin & DeBell 1988;

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nomenclature of vascular plants after Hitchcock and Cronquist 1973). The oldest trees in the forest are about 400-500 years old. The crane is located in the T. T. Munger Research Natural Area at the Wind River Experimental Forest (45°49'N 121°57'W) at an elevation of 355 m. Average annual temperature is 8.8°C, with January and July means of 0°C and 18°C respectively (unpublished climatological summary, Wind River Experimental Forest, 1911-1965). Average annual precipitation is 250 cm.

Methods

At seven locations within the crane circle we sampled canopy density from the ground, vertical transects of epiphytes, and lichen litter. Locations were chosen to represent a range of canopy openness up to medium-sized canopy gaps formed by several large dead trees. Light profiles were collected as a separate data set and thus were not co-located with the vertical transects of epiphytes.

Canopy density

We measured canopy density as viewed from the ground at the base of each vertical transect. Sixteen spherical densiometer readings, four at each of four locations near the perimeter of a 2-m radius circle, were averaged to estimate percent canopy closure. A vertical photograph with a wide-angle (38 mm) lens supplemented the densiometer readings. The photographs were scored for percent canopy cover and provided a view of each vertical profile from the ground.

Light profiles

Photosynthetically active radiation (PAR) light profiles were taken along sixteen vertical transects. These were chosen to be spatially dispersed, representing a range of canopy closure. Several of the profiles extended through gaps in the upper canopy caused by the death of several large trees. Details of our PAR sampling are given in Parker (1997). PAR was measured at high sun angles in clear weather.

Epiphyte profiles

The vertical profile of epiphytes was determined at 7 locations. At each location two observers simultaneously completed vertical transects from the crane gondola, with one observer facing northeast and the other facing southwest, for a total of 14 vertical transects. Each observer estimated percent cover of each functional group at 5 m intervals beginning 5 m from the ground. Transects continued through the highest 5 m mark with visible epiphytes (55-60 m above ground level). A 50 cm X 10 cm quadrat held horizontally at eye level and arm's length was used to estimate cover in the two-dimensional view.

Definition of functional groups (bryophytes, cyanolichens, alectorioid lichens, and "other" macrolichens) follows McCune (1993). The groups are functional, as opposed to taxonomic, because the members of a group share ecological, functional roles more than do members of different groups. Their ecological roles include nutrient cycling, who eats them, microhabitats occupied, and responses to air pollutants.

"Cyanolichens" include all macrolichens with a cyanobacterium as a primary or secondary photobiont. At the crane site cyanolichens are mainly *Lobaria oregana*, with smaller amounts of other *Lobaria* species, *Nephroma, Peltigera*, and *Pseudocyphellaria* (nomenclature of lichens follows Esslinger and Egan 1995). Functionally these genera are related by their N-fixation and their sensitivity to air pollution (e.g., Richardson 1988).

"Alectorioid" lichens include all pendulous species in *Alectoria, Bryoria*, and *Usnea*; in this case, mainly *Alectoria sarmentosa*. In addition to having similar growth forms, *Alectoria* and *Bryoria* tend to be preferred food species for flying squirrels (C. Maser et al. 1986, Z. Maser et al. 1985), deer (Stevenson 1978), and mountain caribou (Edwards et al. 1960, Rominger and Oldemeyer 1989, Servheen and Lyon 1989).

The group "other lichens" includes all remaining macrolichens, mainly *Platismatia* and *Hypogymnia* species. These species do not fix nitrogen, they have less well documented relationships to wildlife, and they have varied sensitivities to air pollutants. In this case, most species are foliose, light-colored above, and contain atranorin in the cortex.

"Bryophytes" includes all bryophytes, but probably overlooking some small leafy liverworts and pleurocarpous mosses that contribute little to the total biomass. Although there is certainly ecological diversity within bryophytes (During 1992, Grime et al. 1990), in general the epiphytic species are ecologically more similar to each other

than they are to lichens, as shown by their tendency to cluster together in analyses that include both bryophytes and lichens (e.g. McCune and Antos 1982). The predominant bryophytes in this study were *Antitrichia curtipendula*, *Dicranum fuscescens*, *Hypnum circinale*, and *Isothecium myosuroides*, (nomenclature of mosses follows Anderson et al. 1990).

To reduce variability among observers, we practiced evaluating cover with a simulated canopy "scene" of epiphyte-covered branches. Although there was considerable variation in the absolute cover values recorded for each functional group, relative values were fairly consistent between observers.

Percent cover values from each transect were converted to relative cover of each functional group at each height. This conversion allowed comparisons between transects made at varying distances from the trees and reduced between-observer differences in cover estimates. To represent the general distribution of epiphytes within the stand, the "overall average" relative covers for each group were calculated as the average relative cover over all transects at each height.

To compare vertical distributions of epiphytes with canopy density and PAR profiles, we calculated "95% distribution limits" for each functional group in each transect. These limits define the portion of the vertical profile that includes 95% of the relative cover of a functional group. We used this method, rather than the total range of a functional group, to reduce the statistical influence of any small, outlying patches of a given functional group. To calculate the limits, we treated the relative cover values of each functional group as histograms with bars centered at 5 m intervals; 2.5% of the total area represented by a given histogram was then subtracted from each end of the distribution, yielding height cutoffs for the middle 95% of the "total relative cover" of each functional group. The analysis was limited to heights between 5 and 55 m (the heights surveyed by all observers).

Epiphyte litter

Epiphytic lichen litter was collected in April 1996 from the forest floor at the base of the seven vertical transects. The purpose of these data was not to estimate total annual litterfall, but rather to estimate in-situ epiphyte biomass. Besides providing a basic description of canopy lichens, we used the relative abundance of functional groups as a check on data quality obtained from the crane. Two, 2-m radius plots were sampled at each site using the method of McCune (1994). Bryophytes were not included because of problems described by McCune (1994). Litter was sorted by functional group during collecting. Samples were oven dried at 60°C for over 24 hours, then weighed to the nearest milligram.

A previous litter sample in August 1994 included 15 plots at 40 m spacings on transects through the crane circle. Processing was similar to the samples below the vertical transects.

Results and Discussion

Canopy density

Canopy density varied over a narrow range, from 81-93% canopy closure. The estimates of canopy density for each transect site were reliable, based on an observed standard error of only 2-6% of the mean. Canopy density was not, however, correlated with the variation in the vertical profile of epiphytes.

Ground-based canopy density measurements were insufficient to characterize the openness of the vertical transects, because of interference from understory vegetation. Most of the gaps, when viewed from above, were carpeted with an understory of *Tsuga* and shrubs, so that even though there might be a large cylindrical opening in the canopy, it would not be reliably detected from the ground.

Light profiles

Transmittance profiles of photosynthetically active radiation (Parker 1997) showed abrupt transitions from bright (over 75% transmittance) to dark (typically less than 25% transmittance) between 13 and 37 m above the ground at 16 sites throughout the study area. The height at which light levels declined below 50% transmittance was generally found in this mid-canopy region. The breadth of this light transition zone (Figure 1A) aptly describes the uneven filling of the mid to upper canopy.

Epiphyte profiles

The relative abundance of bryophytes, cyanolichens, alectorioid lichens and other lichens was

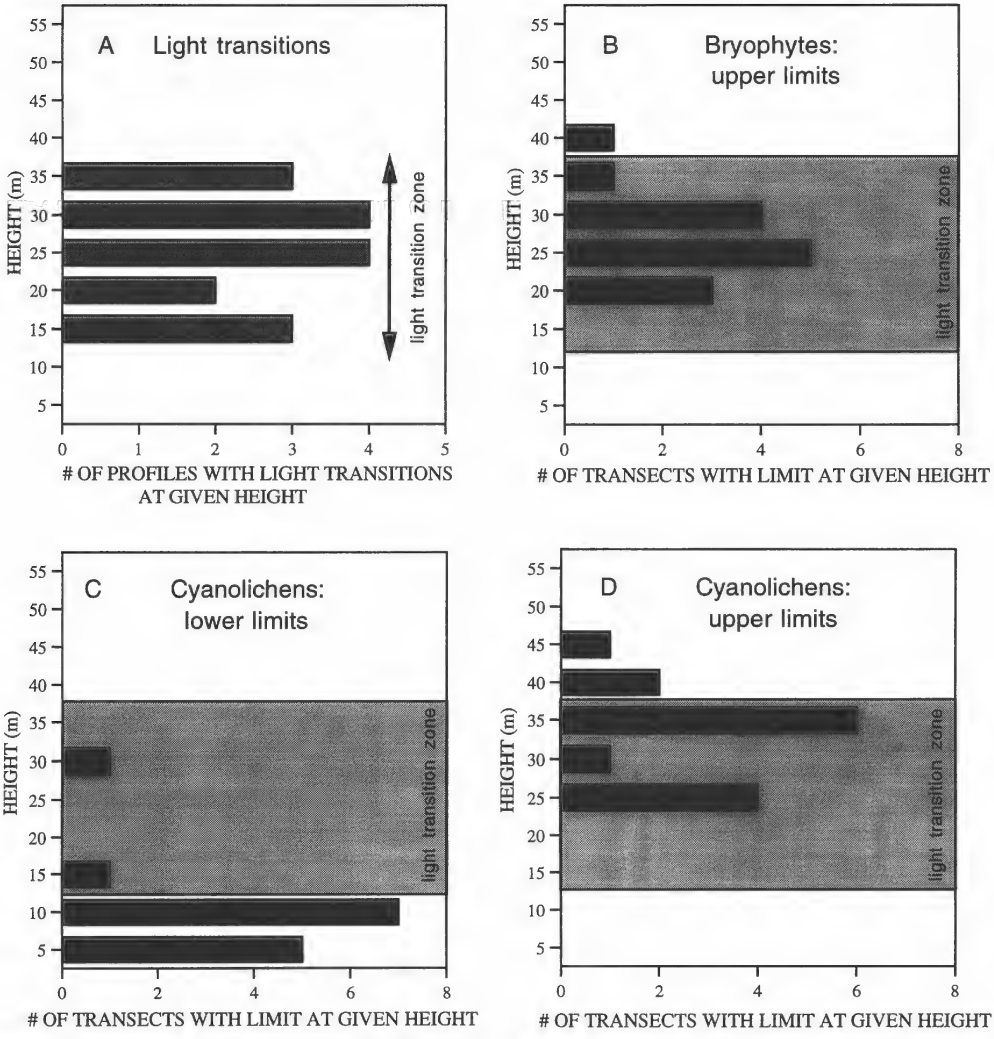
A Light transitions
HEIGHT (m)
light transition zone
OF PROFILES WITH LIGHT TRANSITIONS AT GIVEN HEIGHT
B Bryophytes: upper limits
light transition zone
OF TRANSECTS WITH LIMIT AT GIVEN HEIGHT
C Cyanolichens: lower limits
light transition zone
OF TRANSECTS WITH LIMIT AT GIVEN HEIGHT
D Cyanolichens: upper limits
light transition zone
OF TRANSECTS WITH LIMIT AT GIVEN HEIGHT

Figure 1. Comparison of the locations of the light transition zone and the upper and lower limits of epiphytes. A. Frequency distribution of the height at which light declined below 50% (n=16 transects) with the light transition zone indicated. B-D. Distribution limits of epiphytes (n=14 transects for each graph) compared to the light transition zone. B. Upper limits of bryophytes. C. Lower limits of cyanolichens. D. Upper limits of cyanolichens.

clearly stratified by height. The stratification was apparent in both the individual transect profiles and in the profile of the combined transect data (Figure 2). The pattern was generally comparable with what has been reported previously for other areas (McCune 1993). However, unlike those results, cyanolichens (mainly *Lobaria oregana*) never quite achieved dominance over other groups.

"Other lichens" were spread throughout the vertical gradient and were highly variable in total abundance, with less of a distinct peak as compared with other functional groups. At lower levels, *Sphaerophorus* contributed most of the "other" biomass while green-algal foliose genera such as *Hypogymnia* and *Platismatia* comprised most of the "other" biomass at higher points. Better reso-

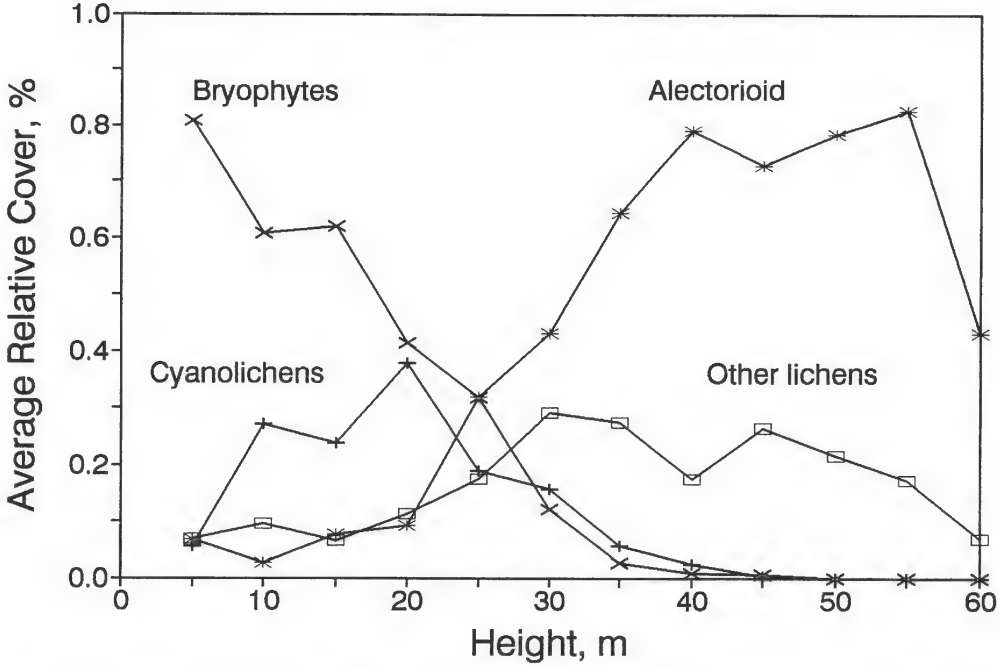

Figure 2. Average relative cover as a function of height in the forest canopy. Relative cover was averaged across all transects for a given height (n=14 transects).

lution of the vertical distribution of "other" lichens might be obtained by dividing this group into two more ecologically similar groups: tufted fruticose (*Sphaerophorus* and *Cladonia*) in contrast to green-algal foliose lichens (*Hypogymnia* and *Platismatia*).

The location of the light transition zone was related to the distribution limits of at least two of the functional groups. The upper limits of the bryophytes (mainly *Isothecium myosuroides* and *Antitrichia curtipendula*) usually fell in the middle of the light transition zone (Figure 1). The upper limits of the cyanolichens straddled the upper end of the light transition zone, and the lower limits of cyanolichens fell on or just below the light transition zone (Figure 1). In other words, cyanolichens were concentrated in the light transition zone, and bryophytes were concentrated below the middle of the light transition zone.

No consistent difference between northeast and southwest facing transects could be discerned. Furthermore, we found no obvious differences in the vertical gradient between dense and more open areas. To examine this point adequately, however, we need canopy closure data from above the ground (see "canopy density" above), preferably a series of observations along the length of each transect.

There were numerous sources of variation in our sampling. Some resulted from the use of different observers for each transect. Variation in the distance between the observer and the trees also introduced a bias, depending on visibility of functional groups. As distance of observation increased, "other" lichens and cyanolichens became more difficult to see than alectorioid lichens.

To minimize these problems, we suggest that future studies use a larger number of transects and a single observer. Using a consistent distance between observers and the trees might also reduce variation between transects.

Epiphyte litter

The total biomass of epiphytic macrolichens was about 1.3 tons/ha (dry mass). The result was based on the August litter sample, using a 100:1 ratio for in-situ:litter biomass (McCune 1994). That

ratio was developed based on a late-summer litter sampling. Lichen litter is typically maximal following winter storms but declines through the summer (Esseen 1985, Stevenson & Rochelle 1984). Had we used the April litter sample our estimate would have been 3.3 tons/ha, about 2-3X too high.

The biomass of epiphytic macrolichens based on the April sample was approximately 42% cyanolichens, 28% alectorioid lichens, and 30% other lichens (Table 1). Because the adequacy of the April sample was considerably better than the August sample (see ratio of standard error to mean in Table 1), these percentages are probably more reliable than those based on the August sample. A ratio of standard error to mean of 10-20% is often used as a rule-of-thumb for sample adequacy in describing ecological quantities (McCune and Menges 1986).

The fairly high percentage of cyanolichens in both the August and April samples was somewhat surprising, since alectorioid lichens are the most conspicuous group of epiphytes at the crane site. Cyanolichens are, however, considerably heavier per unit volume of thallus than alectorioid lichens.

Comparison with other vertical profiles

The forest at the crane site has a vertical profile of epiphytes typical of old-growth *Pseudotsuga-Tsuga* forests at low to mid elevations in the Cascades. Cyanolichens are, however, less abundant at the crane site than in similar-aged stands at the H. J. Andrews Experimental Forest in the Oregon Cascades (McCune 1993, Pike et al. 1975). At the Andrews Forest the biomass of cyanolichens is four times that of alectorioid lichens (McCune 1993), while at the crane site, the biomass of cyanolichens is only 1-1.5 times the biomass of alectorioid lichens (Table 1). The upper limit of cyanolichens is also somewhat lower than in comparable aged stands at the Andrews Forest, reflecting the somewhat drier character of the vegetation at the canopy crane site. Despite slightly higher precipitation at the crane site than at the Andrews Forest, the valley has an overall south-facing aspect and is subject to more frequent penetration of dry air masses from east of the Cascades, owing to the proximity of the crane to the Columbia Gorge (J. Franklin, pers. comm., 1996).

The forest in the Middle Fork of the Santiam Wilderness that Sillett (1994, 1995) studied is both older and wetter than forests at both the Andrews and Wind River Experimental Forests. In keeping with the "similar gradient hypothesis" (McCune 1993), the very old, wet, Santiam forest has a larger total biomass of cyanolichens than at the crane site, and cyanolichens dominate almost to the tops of the trees. Bryophytes are likewise well developed and form large cushions very high in the trees. The very old age and high precipitation

TABLE 1. Proportionate contributions of functional groups of epiphytes to biomass and cover, based on litterfall and vertical profile sampling. "Top" means that the group is abundant at the top of the profile, the actual height varying with the height of the canopy. "Base" means that the group is abundant to the base of the profile, even though sampling stopped at 5 m.

	Bryophytes	Cyanolichens	Alectorioid lichens	Other lichens
LITTERFALL				
Estimated biomass in canopy, kg/ha[1]	no data	1401	934	981
Percent of lichen biomass, April	—	42	28	30
Percent of lichen biomass, August	—	33	33	34
Standard Error/Mean, April, %	—	22	14	11
Standard Error/Mean, August, %	—	29	30	14
CRITICAL HEIGHTS				
Upper limit, average (st. dev.), m	28 (6)	34 (6)	top	top
Lower limit, average (st. dev.), m	base	9 (6)	22 (11)	13 (9)
AVERAGE RELATIVE COVER, %	27 (13)	17 (3)	58 (8)	25 (10)

[1]Based on August sample

allowed epiphytes to advance to the point where functional groups typically found low in the profile have successfully invaded the upper canopy.

We still have large gaps in our knowledge of how the vertical profile varies across the landscape. The vertical gradients in coastal *Picea* and *Pseudotsuga* forests have not been studied systematically. The conspicuous elevational gradient in the abundance of cyanolichens and alectorioid lichens has also not been documented, much less how the vertical profile changes with elevation. We also have limited understanding of how the change in epiphyte environment (temperature, relative humidity, heat load, potential evapotranspiration) change with forest age and site conditions.

Furthermore, we still need to understand the within-stand variation in vertical profiles. Specifically we need to explore how the vertical profile in the distribution of species expands or compresses depending on forest structure. Forest management under the Northwest Forest Plan will produce variable spacing of remnant trees. This spacing is expected to influence development of canopy epiphytes. Two ways to anticipate the result of different spacings among remnant trees are (1) to document how the vertical stratification of epiphytes differs between vertical transects through different local canopy densities and (2) to examine environmental and community changes in canopy remnants after different patterns of logging.

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Northwest Science Forum

Northwest Science Forum provides an opportunity to articulate and discuss scientific issues in a less structured format than peer-reviewed articles. The Forum publishes short articles, opinion pieces, and letters with a focus on science and natural resource issues in the Pacific Northwest. Although the Forum is not peer-reviewed, it is edited for format and clarity. Articles should generally be less than 2000 words and contain minimal literature citations. Letters in response to articles are particularly encouraged; the original author will normally be given a chance to respond to the letter as well. There are no page charges or reprints associated with the Forum, and participants need not be members of the Northwest Scientific Association. Please send all submissions, including two hard copies and an electronic copy (any recent version of Word or WordPerfect) to the Editor.

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The Severe Weather Wildfire—Too Hot To Handle?

Whether the weather is cold
Or whether the weather is hot
We must weather the weather
Whatever the weather
Whether we like it or not

This clever limerick of unknown origin, told to me decades ago by my college fire professor, laments the uncontrollable nature of weather. Recently, statements of the inevitability of catastrophic wildfires under severe weather revived the memory of that poem. These claims, that I will call the "weather hypothesis," suggest that large, severe fires are driven by extreme weather events and intensely burn through forests regardless of the condition of their fuels. One implication of this hypothesis is that fuel treatments are therefore useless as a preventive measure against such wildfires. It is time to clarify the relative role of fuels and weather in wildfires and to evaluate the role of silvicultural treatments in mitigating the hazard of severe wildfires.

Let us first define some terms and phrases commonly used in these debates. A *large* wildfire is one of great size; the word does not imply, in and of itself, catastrophe or damage of any kind. *High-intensity* and *low-intensity* fires define energy release rates; these are physical descriptors of the fire, not its ecological effects. *High-severity* and *low-severity* fire refer to the ecological effects of fires, usually on the dominant organisms of the ecosystem. Large, high-intensity fires are often fires of high-severity; large, low-intensity fires are usually, but not always, fires of low-severity. Some forest types historically had infrequent, high-intensity fires, while other had very frequent, low-intensity fires. In both types of ecosystems, fires could be large. The ecological effects of frequency, intensity, extent, season, and synergistic interactions with other disturbances, such as insects and disease, classified into generalized levels of fire severity, are known as fire regimes (Agee 1993).

Recent statements in the scientific literature and popular press suggest that recent large, severe wildfires in western North America are largely due to extreme weather. The long-accepted view of fire behavior as a function of fuels, weather, and topography has changed for some from an equilateral fire triangle, where each factor can be significant, to a distorted isosceles triangle with the wide base being the weather contribution to fire behavior. This "weather hypothesis", that all

large, severe wildfires are more weather-dependent than fuel-dependent, is found in statements such as the following:

> Forest fire behavior is determined primarily by weather variation among years rather than fuel variation associated with stand age. (Bessie and Johnson 1995)

> Fire behavior should be directly related to regional patterns of weather that influence fuel moisture contents and wind speeds, rather than ecosystem properties that affect fuel loads and structure. (Bessie and Johnson 1995)

> There is increasing evidence that climatic conditions such as severe drought, not fuels, ultimately control fire size and intensity...The point is that climatic conditions are the most important factor in nearly all large fires. (*Cascadia Times,* May, 1996)

> ...thinning has done little to slow the spread or intensity of flames in most big western fires.... In most big fires "there is no relationship between the condition of the stand before the fire, and whether it burns or not"... (*Portland Oregonian,* January 12, 1997)

While the two latter statements may not flow directly from the Bessie and Johnson paper, people discussing this topic with me have cited this paper as evidence for the "weather hypothesis." Bessie and Johnson do an excellent job in establishing weather as a primary factor affecting wildfire size in subalpine forests near the boreal forest ecotone in Alberta, and the title of their paper clearly states that it focuses on subalpine forests. As none of the tree dominants are fire-resistant (all are thin-barked), these fires are also high-severity fires. However, the implied generality of some statements in the paper have encouraged others, including those quoted in the popular press, to conclude that the results of this study are applicable everywhere. Evidence from studies in other areas suggests that these statements should not be generalized to all forest types.

Let's examine three forest types where the "weather hypothesis" might be evaluated, and reasons why it may or may not fit each type. The first two are forest types where the "weather hypothesis" might be accepted: western subalpine forests, and moist coastal forests of Douglas-fir (*Pseudotsuga menziesii*)/western hemlock (*Tsuga heterophylla*), both with a historically high-severity fire regime. The third forest type is widespread in the western U.S.: mixed-conifer, with a variety of dry-site conifers present, usually with ponderosa pine (*Pinus ponderosa*) as a dominant, and Douglas-fir, white fir (*Abies concolor*), or grand fir (*Abies grandis*) as possible codominants in this historically low-severity fire regime. Here the "weather hypothesis" is clearly refuted in favor of what might be called the "fuel hypothesis": reduction of fuels limits fire severity.

The "weather hypothesis" can be accepted for subalpine forests, where fires are infrequent, often intense, and of high-severity. Fire behavior in subalpine forests is complicated by the erratic, often weather-driven nature of these fires (Agee 1993). Fire behavior in average years does appear to be affected by forest structure (Romme and Despain 1989); older stands support crown fire, while younger stands do not. The 1972-1987 experience with natural fires at Yellowstone suggests that fuels were a significant variable affecting fire behavior. However, in long fire-return interval ecosystems like Yellowstone, most of the area burned over past centuries was concentrated in just a few years (Romme 1982). The year of extreme weather, such as 1988, will result in much more area burned and a behavior seemingly independent of the fuel situation (Agee 1993, Bessie and Johnson 1995). As none of the tree dominants are fire-resistant, large fires, being intense and often crowning, are also severe fires. In the long run, regional weather patterns are critically important, and the "weather hypothesis" can be accepted here.

In Douglas-fir/western hemlock forests, fires are infrequent, often intense, and usually of high-severity, although fire behavior will vary by stand age (Agee and Huff 1987, Agee 1993). Early seral stages are most flammable, and can support a "vicious cycle" (Isaac 1940) of reburns, with each reburn fostering thicker stands of flammable bracken fern (*Pteridium aquilinum*). Large burns such the 1902 Yacolt fire (Washington) and 1933 Tillamook fire (Oregon) have reburned in part 4-6 times, mostly from human causes. While this evidence supports a "fuel hypothesis," the early seral flammable stage is a brief window of time in this forest type. While fuel dynamics differ over the rest of the sere, large fire events are probably the result of short-term but extreme changes in drought, lightning frequency, or east (foehn) wind patterns (Agee 1993). With the evidence we now have available, the "weather hypothesis" appears to fit better than a "fuels hypothesis" in this forest type, although not as clearly as in subalpine forests. Fuels are an important factor in fire behavior, particularly in early seral stages, but fuel differences appear to be overwhelmed

by extreme weather in significant, large fire events in older Douglas-fir/western hemlock forests.

While the first two forest types might suggest that the "weather hypothesis" in indeed robust, the third forest type provides ample evidence that fire severity, even in large fires, can be fuel dependent. Mixed-conifer forests of several types that have ponderosa pine as a dominant had a historical fire regime of frequent fires, typically of low-intensity and low-severity (Agee 1993). Forest stands were open, had low fuel loads, and large gaps between surface fuels and tree crowns. If any forest type had the "friendly flame", this was the one: fire, by consuming fuel at frequent intervals, limited the intensity and severity of the next fire. We know from tree-ring reconstructions that fires in these forests were frequent (Dieterich 1980, Savage and Swetnam 1990, Wright 1996). The presence of large, multiple-scarred pines and associated thick-barked species strongly implies that low-intensity, low-severity fires occurred over centuries and included many severe fire weather episodes. While fire severity appears to have remained low even in the presence of severe weather, fire size (independent of severity) may have been larger under regional weather patterns that fostered fire spread (Swetnam and Betancourt 1990).

Fire exclusion during the 20th century has altered landscape architecture, linking high fuel loads vertically within stands and spatially across the landscape. Fireline intensity has increased in mixed-conifer forests, with crown fires more common and 100% tree mortality now common. While it is true that *today*, large, severe fires in these forest types are driven by extreme weather that overwhelms fire suppression forces, this is not the pattern of the past, and statements such as those quoted at the beginning of this paper do not apply to forest structures that occurred historically and for which we *could* manage in the future: sustainable, firesafe, visually beautiful forests of large, widespread trees with ground carpets of wildflowers. Our fire severity problems in these dry forests are not inevitability the result of severe weather but are a legacy of our misguided 20th century forest management over millions of hectares of the western United States.

Salvage logging, such as that authorized by the recent "salvage rider" legislation in Congress, has been proposed as a solution to reduce fuel ladders that result in high-severity fires in forests that historically experienced low-severity fires. First of all, "salvage" is a poor word to use in describing forest restoration treatments: it conjures up the auto junkyard, where pieces of cars are removed before the residual is crushed and recycled. Secondly, if we change only the name of logging operations without attention to the factors affecting fire intensity and severity, the fire severity problem may just get worse.

Can logging fuel-laden forests help reduce fire severity? Some critics have cited Weatherspoon and Skinner (1995) as evidence that doing no forest treatment for fuels in these drier forests might be the best treatment. Weatherspoon and Skinner evaluated the 1987 fires in northwestern California and defined damage by crown scorch evident on aerial photos, a fairly direct measure of severity (not intensity). Over the ranges of forest types they evaluated, the found the least damage in old-growth, unlogged stands, with more damage in partially-cut stands, and the most damage in partially-cut stands that had no post-logging fuel treatment. The partial-cuts they evaluated were typically overstory removals, where the large trees were removed, leaving smaller trees. Even if fire intensity did not vary across unlogged and logged stands, damage would be greater in the logged stands because smaller residual trees will have thinner bark and crowns closer to the ground, making them more susceptible to cambial damage, crown scorch, and mortality from fire. The major implication of this study is less an argument against logging than an argument against the types of logging and fuel treatments that were done in the past. To reduce fire damage from wildfires, future thinning operations must concentrate on small trees with operations called low thinning, removing the trees that have invaded these sites since fire exclusion began, and cleaning up the debris. Markets now exist for much of this small material, and if a steady supply were available new mills could be built, providing jobs and restoring forests simultaneously (heaven forbid, possibly a win-win situation!). By leaving the largest trees and treating fuels, fire tolerant forest conditions are created, so that fire severity can be significantly reduced. This is not salvage, but restoration.

Secretary of the Interior Bruce Babbitt made a historic speech in February, 1997, calling for

changes in Federal fire policy, and landscape-level forest treatment to reduce wildfire hazards, including thinning and prescribed burning. These treatments are sensible where a "fuel hypothesis" is valid, in our drier forests with low-severity fire regimes where ponderosa pine was dominant or codominant, but they must be applied with attention to those factors affecting fire intensity and severity (van Wagtendonk 1996). Such treatments are probably least valid in subalpine forests, coastal forests, and other high-severity fire regimes, where the "weather hypothesis" appears more likely to be valid.

Attempts to apply either the "fuel hypothesis" or "weather hypothesis" to all western landscapes are as misguided as our now-abandoned attempts this century to develop a grand, unified model of plant succession. Ironically, it was the presence of disturbance in ecosystems, and the inability of rigid models to address disturbance, that ended the search for the unified plant succession model. Let us not repeat the same mistake now with our views on disturbance in ecosystems: there is not a one-size-fits-all approach. Although the physical principles of fire apply everywhere, different forest types with unique organisms and fuel types, and differing environments, will assure that fire behavior will have a range of important contributing factors: not always fuel, not always weather. That old limerick probably needs to be updated:

Whether the weather is cold
Or whether the weather is hot
Topography and fuels
Are part of the rules
Whether we like it or not

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Book Reviews

Rights to Nature: Ecological, Economic, Cultural, and Political Principles of Institutions for the Environment

Susan S. Hanna, Carl Folke, and Karl-Göran Mäler, eds., Island Press ($29.95)

Rights to Nature is another of the generally well-received books published by Island Press covering issues in environmental policy. This volume presents a series of articles dealing with the relationship between different kinds of property rights and their effects on natural resources and ecological systems. This topic is timely, as individuals, communities, and societies try to define their relation to nature in a sustainable manner.

The book is an outcome of a research program sponsored by the Beijer International Institute of Ecological Economics, an institution organized under the auspices of the Royal Swedish Academy of Sciences. A major goal of the research program was to join social scientists with ecologists and other natural scientists in the study of property rights and their effects on natural systems. The book's editors, Susan Hanna, Carl Folke, and Karl-Göran Mäler, state their position on the importance of this issue by asserting, in their introductory chapter, that "environmental problems arise from incomplete and asymmetric information combined with incomplete, inconsistent, or unenforced property rights."

The book is organized in four parts. The first covers the interface between social and ecological systems; the second covers the structure and formation of property rights; the third covers culture, economic development, and property rights; and the fourth covers property rights at different scales.

In the first part, contributors Robert Costanza and Carl Folke lead off with a review of major concepts and findings of ecological science that are relevant to human management and property rights. Co-editor Hanna and Svein Jentoft follow with an overview of human use of the environment, including evolving attitudes, types of valuation, and types of social organization. C S Holling and Steven Sanderson offer an elegant model of the dynamics of complex ecological and human social systems. They use Holling's renewal cycle of exploitation, conservation, release, and reorganization, as originally postulated for ecosystems, and apply these ideas to social structure and change. They review, as well, related theories of human social dynamics. Fikret Berkes closes this part with a prelude to themes dominating the remainder of the book: types and attributes of property rights regimes, a view of how human-made, natural, and cultural "capital" are related, and suggestions for evaluating the performance of property rights implementations.

The second part begins with a chapter by Bonnie McKay that carefully defines types of property and distinguishes these from types of management. Elinor Ostrom and Edella Schlager follow with a helpful model of a hierarchy of types of property rights and a scheme for labelling holders of these rights. They distinguish between the operational rights of (1) access to, and (2) withdrawal of, resource units, and the collective choice rights of (3) management of use of resources, (4) exclusion of others from resources, and (5) alienation, or the right to "sell" other rights in a resource. Arranged as a hierarchy, each successive right includes all previous. Thráinn Eggertsson concludes this part with a discussion of the economics of control, that is, how costs of exclusion (of non-owners) and costs of governance complicate traditional benefit-cost analysis.

The third part has two articles that discuss pertinent case studies of attempts to institute property rights based on European and North American models into Africa and India, respectively. Jean Ensminger reports on failures of the Swinnerton plan for land titling in Kenya to deliver on expectations, failures due in many respects to inadequate attention to cultural practice and tradition, but also to economic inadequacies. Narpat Jodha describes another 20th century attempt at land reform, this case in India. This effort has also largely failed to secure better management of common resources, and for similar reasons of lack of incorporation of some of the more useful features of traditional management.

In the fourth part, Margaret McKean begins with a discussion of types of goods according to

whether they are "subtractible" (depletable) or not, and whether it is easy to effect exclusion or not. She then continues with some advantages of common property for resource management, and finishes with an example of resource partitioning through common property management in a case study in Japan. Oran Young discusses aspects of international governance of resources. The book's concluding chapter by Scott Barrett contains the only technical material, an interesting method for analyzing the allocation of rights to transboundary resources, treated as a bargaining game.

For readers interested in property rights and natural resources, this book provides a reasonable introduction to the issues and literature in economics, political science, and anthropology. The material presented on ecology is necessarily a broad summary, though I found the Holling and Sanderson chapter to be the most wide-ranging and stimulating piece in the book. Within social science, the views represented are of a somewhat limited group it appears, those who have been actively researching the property rights issues and building on each other's work. The commonality is evident from the numerous reciprocal citations among the authors and a common framework of definitions for the key concepts of property rights.

The editors did not include any contributions by other social scientists, for example, geographers, or by legal scholars or philosophers. One complementary approach to property rights focusing on the philosophical basis for, and the political establishment of, land policy is *Policy for Land: Law and Ethics* by Lynton Caldwell and Kristin Shrader-Frechette. Readers should also not confuse this book with the very similarly titled *The Rights of Nature* by Roderick Nash, a history of environmental ethics. An important question, indeed, is whether the "rights to nature" approach can be completely successful without consideration of the "rights of nature".

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Lost Landscapes and Failed Economies—The Search for a Value of Place

Thomas Michael Power, Island Press, Washington, D.C.

Proponents of "folk economics" would contend that the extraction and processing of natural resources lies at the heart of economic development. Not so, insists Thomas Michael Power in his lucid and well-documented book *Lost landscapes and Failed Economies.* The key thesis of this work is that the premise of "Folk Economics," which asserts that extraction and processing of natural resources are the heart of economic development, can be proved to be false based on economic research and the analysis of abundant empirical facts. Power effectively uses data, charts and simple computations to illustrate arguments and examples, all of which are put forth in a style easily understood by the non-economist. He uses current examples to examine jobs-versus-the-environment arguments and soundly debunks common beliefs held by many amateur economists. This book is written for the non-professional economist but is well grounded in the economic literature.

The fact that this book deals clearly and efficiently with the economics of destructive (i.e. extractive) and non-destructive uses of natural resources makes it a logical starting point for scientists interested in interdisciplinary research that includes economics. Human economies, after all, are responsible for most of the destructive and widespread disturbances on the face of the earth. Understanding the origins, ontogeny and current trajectories of these economies, particularly those in North America, gives the reader the perspective needed to evaluate economic arguments affecting environmental issues. Throughout the book, Power cautions that we as a society should avoid becoming "hypnotized by the rear view mirror"—meaning that it is not appropriate to project future economic trends based on past performance, without regard for drastic and vital changes in the economic engines now driving our economies. He argues that there are broad-ranging economic forces afoot that more than offset the effects of jobs lost in extractive and heavy industries, forces that can offer families and communities a new sense of well-being.

Mining, logging and agriculture are the three extractive industries discussed in this book; two chapters are devoted to each topic. Power examines the widely held notion that metal mining employment is a fundamental component of many western economies. Since 1980 employment in this field has declined by 25,000 jobs while the rest of the western economy has increased by 6.9 million jobs (Fig. 4-7). In 1990 metal mining accounted for about 0.1% of the total employment in the West. These statistics are strong evidence that the old model (view from the rear view mirror) is not a suitable model for the future—economies are changing. The book examines the environmental degradation associated with mineral extraction activities and argues that natural landscapes house different resources with different values. The author asserts that "there is nothing in economic theory or empirical economic experience to suggest that commercial economic value is always greater than non commercial economic value. In fact, this is often not the case." Later on, he develops this idea further.

Logging examples are similar to those for mineral extraction. Community dependence on timber, as with mineral mining dependence, has resulted in a boom and bust economic roller-coaster, historically. Since 1969 in the Pacific Northwest, wood product employment has declined by 35,000 jobs but the economy as a whole has expanded by 500,000 jobs during the same period (Fig. 6-4). The facts suggest that automated harvesting techniques have accounted for many of the lost jobs, not just the restriction on harvesting due to environmental concerns. The author pulls no punches when he states that "..it is not the time-honored profession passed down from generation to generation (that is being threatened by downsizing the wood products industry) but rather high paying jobs for relatively uneducated white males." Obviously, not all of the author's generalizations regarding economics at the national scale apply to the Pacific Northwest at the regional scale. Further, while many communities can rebound from the closure of wood product related industries by diversification into other economic activities, some communities, particularly the smaller and more isolated ones, may be devastated.

The chapters on agriculture discussions focus on grazing on federal land and federal subsidies for farming, including irrigation and pest (coyote and prairie dog) control. The irrigation subsidy

is discussed in greatest depth, with excellent summary information and examples. One interesting point made is that in Arizona, water used to irrigate livestock forage and feed grain contributes only one thirteenth of one percent as much to personal income as the same quantity of water used for manufacturing, trade, transportation or services would contribute. The author failed to discuss one of the major environmental catastrophes associated with irrigation: soil salination. This agricultural phenomenon dates back five millennia to the time of the Sumerians, whose salination of the soil via irrigation is believed to have contributed significantly to the decline of their civilization.

The book ends with a very positive and thoughtful discussion regarding alternative landscape uses. The summary becomes philosophical as the author examines and compares aspects of economic quality (well-being) vs. income level. The tradeoffs between the two are examined from the perspective of individual choice, with some surprising conclusions. *Lost Landscapes* offers a valuable and well-documented examination of economic issues related to resource extraction that are likely unfamiliar to most environmental scientists. The annotated footnotes and citation list are welcome reference bonuses. Power's book should be read by those non-economists drawn to an interdisciplinary view of the economics of extractive industries....and they will enjoy it!

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Clean Water: The Citizen's Complete Guide to Water Quality and Water Pollution Control
Kenneth M. Vigil, 1996
Columbia Cascade Publishing Company
$16.95

Burgeoning population and industrial growth in the Pacific Northwest and elsewhere in the nation are placing unprecedented demands upon, and threatening the quality of, our most vital natural resource: water. Many of us take for granted the water that we rely upon for almost every aspect of our daily lives. We assume that it will always be there when we want it. However, clean water is a finite resource and one that is continually threatened by various sources of pollution. The Environmental Protection Agency has estimated that about one-third of all the waters assessed by state agencies are unsafe for swimming, fishing, and drinking. Because this vital resource is finite, protecting its quality should be of paramount importance to everyone. But what can we, as ordinary citizens, do to protect our waters? What do we need to protect them from? Aren't there already rules and regulations designed to protect them? While many of us express concern about the use and protection of our nation's waters, we may feel uninformed about the relevant, or even basic, issues that surround water quality.

Issues related to water quality weave together numerous disciplines, including geology, hydrology, chemistry, biology, civil and environmental engineering, and law. Finding answers to even fairly basic questions concerning sources of water, treatment of water, and water-pollution prevention commonly means poring through technical literature in several fields. For the nonspecialist with a technical background, such a task may prove challenging; for the nontechnical person, the task can be daunting.

In *Clean Water*, Kenneth Vigil, an environmental engineer, has compiled and reduced the salient aspects of a wide range of topics from several water-related disciplines into lucid, straightforward prose accessible to everyone, and that is the strength of this book. Vigil's stated purpose for writing this book is that most textbooks on water quality and water pollution have been directed at specific professional audiences, and have focused commonly on a single topic. Because wise use and protection of water is of paramount importance to everyone, he believed that information about water quality and water pollution could, and should, be made more accessible to the general public. He felt that the important topics from a range of disciplines could be summarized in sufficient detail as to be informative, but not so detailed as to overwhelm, and thereby distance, the average citizen. Hence, the book is meant to provide a fundamental education to a very broad audience. It is not intended to replace existing textbooks.

Clean Water is divided neatly into eight chapters. It begins with a discussion of the water environment, and includes such topics as the hydrologic cycle, natural conditions that influence water quality, and water quality concerns. Subsequent chapters delve into practical aspects of water chemistry and microbiology; sources of water pollution; preventing water pollution; water quality regulations; watershed management; drinking water; and ways that we, as ordinary citizens, can protect water quality.

Each chapter in the book concisely ties basic concepts of various disciplines to water quality. To make harder-to-grasp concepts more concrete, simple illustrative examples are employed. For example, to illustrate the concepts of suspended and dissolved solids in water, Vigil has the reader imagine emptying packets of salt and pepper found in restaurants into a few glasses of water. This example also helps the reader grasp the magnitude of quantities reported in milligrams per liter. Technical jargon is introduced only when necessary, and then is clearly defined and explained. For readers whose comprehension or enthusiasm lags when confronted with the numerous acronyms prevalent in the water-quality field there is a comprehensive glossary. Chapters are followed with limited references to the technical literature for those who wish to explore a specific topic in greater detail.

For readers who feel uninformed about basic technical aspects of water quality or of the rules adopted to protect water quality, the chapters on water chemistry and microbiology, and water quality regulations are particularly informative. In the former chapter, the reader learns that water is composed not simply of hydrogen and oxygen atoms; it is also composed of dissolved gases,

dissolved and suspended organic and inorganic substances, solids, and microorganisms. Here, Vigil points out which substances dissolved in water improve its quality, which reduce its quality, and why. The reader also learns to appreciate how apparently benign acts such as discharging moderately warm water into rivers and streams or removing channel-bounding trees can affect aquatic habitat, by understanding the relation between dissolved oxygen and temperature. The chapter on regulations outlines various federal, state, and local regulations that exist to protect the nation's waters. It describes components of various legislative acts, such as the Clean Water Act. The chapter concludes that despite these legislative rules and regulations some attempts to restore and maintain the quality of the nation's waters have fallen short. This conclusion lays a nice foundation for the final chapter that focuses attention on ways that ordinary citizens can protect water quality.

While the book is rich in photographs (with one particularly stunning photograph of whales breaching the sea surface), it is rather light on illustrated figures. A few more simple figures would have enhanced material presentation, particularly when describing some of the more technical aspects of water chemistry and biology. For example, although data regarding the relation between dissolved oxygen and temperature are provided in a table, a simple figure plotting the relation of these data might have had more impact.

As citizens whose everyday activities have an impact on local water quality, everyone would benefit from reading this book. Issues concerning water quality and water supply affect us all, and we can make wise decisions regarding the use and protection of our waters only if we are well informed. Becoming informed citizens is particularly relevant in light of the fact that two of the most important pieces of water quality legislation, the Clean Water Act and the Safe Drinking Water Act, are currently the subject of scrutiny by the U.S. Congress. *Clean Water* provides an easily traveled avenue by which we can become well informed.

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Do Lemmings Commit Suicide? Beautiful Hypotheses and Ugly Facts
Dennis Chitty, Oxford University Press
(CDN $36.95)

The search for causes of the fabled fluctuations of northern microtine rodents has been important in the development of ecology as a scientific discipline. But unlike the story of quantum physics or the discovery of the double helix, this quest has not, as yet, led to an exciting conclusion with profound implications. In fact, alchemy aside, few scientific endeavors have so slimly rewarded with general insights such prolonged investigative effort, and that so much of population ecology touches this talisman is remarkable. This book is an insider's account of these ecological investigations from their beginnings in the 1920s up to the present time, and as such is a valuable contribution to the history of ecology.

The question that obsessed Dennis Chitty and his mentor Charles Elton was: How are animal populations regulated? Today we perhaps understand the question better, but answers remain elusive. As a single current example, landowners and conservation groups in Britain are at odds over whether killing raptors will increase grouse populations, and so improve shooting. A recent account in *The Guardian* (November 27, 1996) could almost have been written as Elton first embarked on his studies more than 70 years ago: 'The six-year study...aims to establish for the first time how grouse and predators interact when left to themselves by gamekeepers. It is being done in great secrecy on the Duke of Buccleuch's Langholm estate in Dumfriesshire.' How is it that ecologists have done so much and accomplished so little?

This ecological tale is recounted in largely chronological sequence, outlining the phenomena, the various investigations, the wartime effort at rodent control, the successive hypotheses to explain cycles, the many failures, and the controversies. The book is best read as an historical account of the period 1920–1960; post-1960 events are relegated to Chapter 12, entitled 'Epilogue, 1961-1995. The book does not do a thorough job with the more recent work, or with synthesizing the current state of scientific affairs. It does provide a highly personal and entertaining view on the sociology of science, with many anecdotes, accounts of the personalities involved, castigations of opponents and colleagues alike, and frequent pulpit-pounding on the proper procedure for gaining scientific knowledge. The irony of the latter will not be lost on most readers. It certainly wasn't on the writer, who manages to remain endearing by being hardest on himself, and being able to enjoy a few jokes at his own expense. Chitty's 'obituary', written by his colleague Peter Larkin, ranks as great humor for it assuages the wound even as it opens it to expose a bit of the painful truth. The book also details—and praises—the important role played by Helen Chitty in all of this work, and it is dedicated to her memory.

In his epilogue Chitty attributes the current disarray of population ecology to (p. 199) a "failure to agree on standards of scientific evidence." I disagree. To my mind it seems that important concepts that will be essential to the eventual solution were simply not available when Chitty and Elton were the leaders in the field. In fact I believe that some of these essential concepts are just now beginning to be comprehended by ecologists. In science, more than in any other human venture, what seems at the time to be blind lurching from one wrong turning to another is often revealed in historical perspective to be a more-or-less orderly examination and rejection of certain ideas in favor of better ones. A good analogy for this ecological history might be made with the successive theories of heat; each was useful in some contexts but later proved powerless in others. Ultimately they were all utterly wrong, but they led to Clausius' thermodynamic laws, to Boltzmann's statistical dynamics, and to quantum physics. With historical back lighting it is the facts that tend to acquire a certain beauty, while every flaw of hypotheses once held as beautiful is thrown into sharp relief.

Chitty is a harsh and penetrating critic. In a review of David Lack's 1966 book *Population Studies of Birds* (*Ecology* 48: 698-701; 1967; see footnotes p. 212), he awarded Lack a one-upmanship prize for asserting that it was too early to draw firm conclusions based on only the first 17 years of his great tit study. But he is equally critical of his own work. In the same review, he wrote "perhaps ecologists of the next generation will be more successful in digging it (the answer) out. They might start by doubting the truth of everything that has so far been written on the

subject, including the ideas of the present reviewer." I doubt whether this would be a good idea, for I suspect that history will be kinder to Chitty's ideas than he has been to his many critics, or to himself. An ongoing process of examining this history is essential, because population ecology is much more important than rearing game birds for sport on the private estates of nobles: Fishes in the ocean commons, insects in the world's crops, endangered species in scattered islands of habitat, and we humans on our tiny planet—all urgently require answers to questions that Chitty and Elton were among the first to ask. A hundred years hence, this little book will help ecologists to look back and understand how we found the answers.

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American Beginnings: The Prehistory and Palaeoecology of Beringia
Frederick Hadleigh West (Ed.), 1996, The University of Chicago Press. (Cloth, $75,00).

In some ways this impressive volume is an update of West's 1981 book, *The Archaeology of Beringia*. The chief difference is that in the earlier volume West was able to synthesize the data himself, whereas this new work is truly a source book containing almost everything any archaeologist or paleoenvironmentalist wants to know about Beringia with chapters written by the foremost researchers in the field. Both relevant older data and data accumulated since 1981 are included. The temporal focus is on the period between 12,000 and 9,000 years ago although coverage extends back to 35,000 in Siberia for obvious reasons.

The volume editor leaves the specific boundaries of Beringia somewhat open, but in an introductory section David Hopkins defines it as the region west of the Mackenzie and east of the Kolyma. The geographic coverage north-south is from the Arctic Ocean to the Alaska panhandle. Somewhat puzzling is the inclusion to two Northwest Coast sites, Hidden Falls and Ground Hog Bay, that are beyond the conventional border of Beringia and lack the distinctive "Campus" microblade cores (wedge-shaped cores made on a biface) that are the most distinctive element of both the eastern (Dyuktai) and western (Denali) segments of the Beringian cultural tradition. Bluefish Cave is the only Yukon site included. The inclusion of a report on the well-dated Ugashik Narrows site on the Alaska Peninsula, which clearly belongs in the Beringian Tradition, would have helped round out the contents.

The volume is organized into three parts. Part One contains 12 substantive chapters on the geology, palynology, paleogeography, paleontology and paleoecology of both Russian and American sides of the strait, and an Introduction by Paul Colinvaux who tells the reader what it is all about. The main paleoenvironmental issue of whether Beringia was a barren unproductive polar desert as can be inferred from the pollen studies, or a productive grassland teaming with megafauna as indicated by the mamalian remains, is unresolved. The possibilities of a mosaic of microenvironments or of vegetational zonation are mentioned as possible resolutions. The problem of contamination of C-14 dates on bone from Arctic sites, which is the subject of a recent paper (*Journal of Archaeological Science* 23, 577-585), was not broached, but may eventually help resolve this issue.

The archaeological evidence is presented in Part Two with three chapters on Western and six on Eastern Beringia and an introductory summary by John Hoffecker. The archaeological remains are described region by region and site by site . Dominating the Western section are descriptions of the sites, mostly along the Aldan River, by Mochanov and Feedoseeva which are the basis for the formulation of the Dyuktai culture. It is very useful to have these now in English. The authors state that all the typical artifacts are illustrated. These authors reject published criticisms of their work that have centered on the acceptability of the C-14 dates on the early (before 18,000 years ago) part of the Dyuktai sequence. Short summaries of other important sites in the Russian Far East are given by several Russian scholars.

In reading the six chapters covering the archaeology of the American portion of Beringia I was impressed by the uniformity in culture content, although there is some variability. Most of the issues center around the interpretation of variability among and between the various artifact assemblages, and the acceptability of various C-14 dates. Comparitive typology and C-14 dates do not always agree. Is the Nenana Complex, which is demonstrably the earliest known segment of the Beringian tradition in North America, truly different from the succeeding Denali Complex or are the observed differences the result of sampling? Scavanging of old ivory by later peoples to make artifacts has been demonstrated at the Broken Mammoth site, and could such scavanging account for the early dates on bone at Bluefish Cave? Did the earliest microblades in Alaska from the Swan Point site dated at 11,660 years ago come from Campus type cores or some other more generalized type of core? How late did the Denali complex persist—to 3000 years ago based on dates from the Campus site that Mobley would like us to believe, or only to 8000 years ago as West insists? The only issue of this sort that is fully resolved is Ranier' s careful

investigation of the field notes from the Putu site which show that the 11,470 C-14 date is not associated with the fluted points or with any of the other cultural remains at the site. More field data plus quantitative and qualitative assessments of both C-14 dates and artifact assemblage content should eventually resolve these issues. This volume contains the data with which to the latter.

The final section contains a chapter by Greenberg promoting his classification of New World languages, and a well reasoned synthesis of the historical relationships of Beringian culture by West, that provides plenty of food for thought. Using comparitive typology West continues to attempt to derive Clovis from the Beringian Tradition.

The data are well presented with numerous excellent illustrations, and the text is well edited, although "gremlins" do intrude here and there. For example, in Fig. 7.5 the numbering of the components in this stratigraphic profile is reversed from what is stated in the text, and in Fig. 12.2 the unifaces numbered 4, 5, and 6 are mixed up so that the type names do not correspond with the type illustrations. However, these minor errors do not detract from this important, timely, attractive volume.

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NORTHWEST SCIENCE

Information for Authors

Scope of Articles

The pages of *Northwest Science* are open to original and fundamental research in the basic, applied, and social sciences. *Northwest Science* does not publish notes or bibliographic papers. All submissions are refereed, usually by two reviewers. Papers are welcome from authors outside of the Pacific Northwest, but at least one author of any paper considered for publication must be a member of the Northwest Scientific Association.

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The manuscript should consist of sections in the following sequence:

- Title Page
- Abstract
- Text (Introduction through Acknowledgments)
- Literature Cited
- Footnotes
- Tables
- Figure Legends
- Figures

Maximum article length for papers published in *Northwest Science* is 16 journal pages. Two typed pages are approximately equal to one journal page.

Numerals will be used to indicate footnotes unless such usage would be confused with numerical data. In this situation, lowercase letters should be used. Do not break, or hyphenate, words at the ends of lines. Words to be italicized should be typed in italics.

The format and style of manuscripts should conform to general usage in recent issues.

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Abstract: The purpose of an abstract is to briefly summarize the study so it is quickly accessible to the general readership of the journal. The abstract, written in complete sentences and not exceeding 250 words, should precede the text on a separate page. Authors are reminded of the diverse disciplines and readership served by the journal. With this in mind the abstract should have three parts of unequal length. First, the abstract should begin with a statement of the purpose of the study that indicates *why the study was undertaken.* Next the experimental design or approach should be stated and the *results summarized.* The abstract should end with a sentence or two on the larger significance of the research. Authors are strongly encouraged to give the abstract proper attention.

Text: Literature citations within the manuscript text should contain the author's name and year of publication, using formats A and B.

- Format A:
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  ...studied by Smith and Brown (1979)...
  ...studied by Smith et al. (1980)... (if more than two authors in a citation)
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...results of other investigations (Smith 1966, 1970; Jones 1973; Brown 1974)...

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Present all data in international (SI) unites. English equivalents may be added parenthetically. Use the 24-hour clock (0600 and 2230) and continental dating (17 November 1986).

On first mention, a species should be designated by common name followed by systematic binomial (italicized). Common names for species should not be capitalized except when derived from a proper name. Thus, "mountain hemlock" or "white-crowned sparrow," but "Douglas-fir" or "Clark's nutcracker." For abbreviations and forms of titles for serial publications, follow the BIOSIS List of Serials. Consult with the Council of Biology Editors *CBE Style Manual,* 4th ed., for general information on manuscript preparation.

Literature Cited: Only the *first letter* of the *first word* of journal articles, technical reports, theses, etc. are capitalized. First letters of *major words* in book titles are capitalized. All authors of a title are listed in the bibliographic citation ("et al." is used only in the body of the text).

Citation of unpublished reports is discouraged. Rather, cite the sources as a personal communication from the senior author (P. W. Smith pers. comm.).

Citations should be double-spaced and listed in alphabetical order at the end of the article. Listed below are some typical citations.

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Broadbooks, H. E. 1970a. Home range and territorial behavior of the yellow pine chipmunk *Eutamius amoenus.* J. Mammal. 51:310-326.

_____. 1970b. Populations of the yellow pine chipmunk, *Eutamius amoenus.* Amer. Midl. Nat. 83:472-488.

Ceska, A., and H. Romer. 1971. A computer program for identifying species group. Vegetatio 20:48-73.

Grizze, J. E., C. F. Starmer, and G. G. Kuch. 1969. Analysis of categorical data by linear models. Biometrics 25:489-504.

Monographs or books

Jennings, H. S. 1906. Behavior of the Lower Organisms. Columbia University Press, New York.

Papers in proceedings or symposia

Ryland, J. S. 1975. Parameters of the lophophore in relation to population structure in a bryozoan community. *In* H. Barnes (ed.) Proc. 9th Eur. Mar. Biol. Symp., Aberdeen University Press, Aberdeen. Pp. 363-393.

Theses, dissertations, personal communications, and articles in press

Donald, D. B. 1971. The limnology of the plankton of three temporary pons in Alberta. University of Calgary, Calgary. M.S. Thesis.

Wiser, H. C. 1961. Decomposition and homogeneity of continua on 2-manifolds. University of Utah, Salt Lake City. Ph.D. Dissertation.

Danwiddie, P. W. In Press. Dichotomous key to conifer foliage in the Pacific Northwest. Northw. Sci.

Technical Bulletins

Daubenmire, R., and J. B. Daubenmire. 1968. Forest vegetation of eastern Washington and northern Idaho. Wash. Agric. Exp. Sta. Tech. Bull. 60. Washington State University. 210 p.

Goodwin, J. G., Jr., and C. R. Hungerford. 1979. Rodent population densities in pine forests. USDA For. Serv. Res. Pap. RM-214. Rocky Mtn. For. Range Exp. Sta., Fort Collins, Colorado. 39 p.

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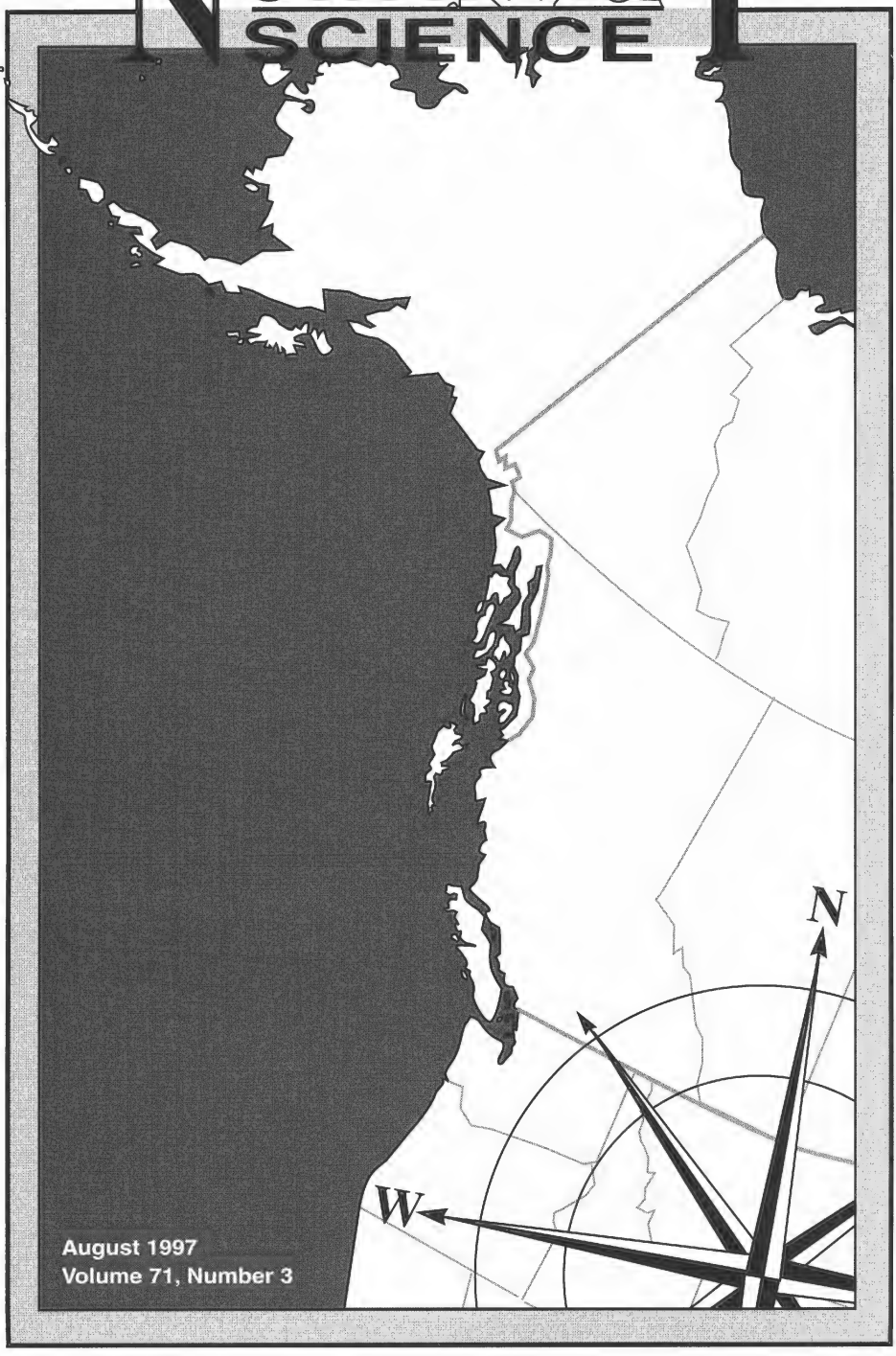
NORTHWEST SCIENCE



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258 Book Review

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The Relationship of Site Index to Synoptic Estimates of Soil Moisture and Nutrients for Western Redcedar (*Thuja plicata*) in Southern Coastal British Columbia

Abstract

We described the pattern of mean site index and the associated variation in site index of western redcedar (*Thuja plicata* Donn. ex D. Don.) in relation to categorical variables of soil moisture and nutrients as identified by the field-procedures of the biogeoclimatic ecosystem classification. Additionally, we compared the site index of western redcedar to that of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.). We sampled 105 plots from stands having western redcedar as the major tree species. The plots were distributed within each of two climates, a drier and a wetter cool mesothermal climate in south coastal British Columbia. Sixty-three plots had both western redcedar and western hemlock available for comparisons. Heights and ages were measured on five dominant trees on a 0.04 ha plot, and the height at a base age of 50 years was calculated to give site index. The highest western redcedar site index occurred on sites identified as having no moisture deficit or excess and high nitrogen availability. Site index decreased on sites identified by field procedures as being outside this optimum moisture and nutrient condition. The mean site index was significantly greater in the drier cool mesothermal climate than the wetter cool mesothermal climate on sites identified as having similar soil moisture and nutrient conditions. Climate appears to have a large effect on site index, therefore, on similar soil conditions the site index of western redcedar may be higher in the southern portion of its range in the United States; and lower in north coastal B.C. and southeastern Alaska. On sites where both western redcedar and western hemlock were sampled, the site index of western redcedar was consistently lower. Based on a northward trend, we may predict that in southeastern Alaska the site index values may be larger for western redcedar compared to western hemlock, while in Washington and Oregon there may be an even greater site index of western hemlock over western redcedar than reported here.

Introduction

Where timber production is the management objective, knowledge of the relationship between the potential productivity of possible tree species to various levels of light, heat, nutrient, moisture and aeration is necessary for decision making on a species- and site-specific basis (Klinka and Feller 1984). For example, foresters need to decide which tree species to use as regeneration for a particular harvested area to obtain maximum sustainable productivity. Similarly, when making decisions whether to apply various silvicultural treatments such as spacing or fertilizing, foresters need to decide whether the potential productivity of a particular site warrants the cost.

In British Columbia, site index (height of specified dominant trees at a reference age, and the most widely accepted indirect estimate of potential forest productivity; Mader 1963; Tesch 1981), is used to develop productivity relationships with site units derived from the biogeoclimatic ecosystem classification (BEC) (Pojar et al. 1987). This classification is currently used as an ecological foundation for all silvicultural activities, and the categorical measures of soil nutrient and moisture conditions have been used to describe and predict site index for Douglas-fir (*Pseudotsuga menziesii*) (Klinka and Carter 1990), western hemlock (*Tsuga heterophylla*) (Kayahara and Pearson 1996) and Sitka spruce (*Picea sitchensis*) (Kayahara and Pearson 1996). These investigations provide a description of mean site index, inferring potential timber productivity, and associated variation in site index for various combinations of soil moisture and soil nutrient conditions. This paper reports the results for western redcedar (*Thuja plicata* Donn. ex D. Don.).

The objectives of this study were to (1) describe the pattern of mean site index and the associated variation in site index of western redcedar in relation to soil moisture and nutrient classes as identified by the field-procedures of the biogeoclimatic ecosystem classification; (2) compare the site index trends for western redcedar between a drier and wetter cool mesothermal climate; and (3) compare the site index of western

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redcedar to that of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.)

Methods

Study Area

The study sites were located in southern coastal British Columbia (latitude 49°20'N, longitude 122°35' to 123°05'W, elevation 160 to 295 m). Plots were located in dry maritime and wet maritime cool mesothermal climates as delineated by the Dry Maritime and Very Wet Maritime Coastal Western Hemlock subzones (CWHdm and CWHvm respectively) of the biogeoclimatic ecosystem classification (Klinka et al. 1991). The climate of the two areas in this study is characterized by cool wet summers and mild wet winters, although hot dry spells are more frequent in the drier area (CWHdm) (Meidinger and Pojar 1991). Mean annual precipitation is 1827 mm for the drier area (CWHdm) and 2787 mm for the wetter area (CWHvm); the mean annual temperature is 9.8°C for the drier area and 8.2°C for the wetter area (Environment Canada 1982). The stands in both subzones originated from logging during the early 1900's followed by fires. The natural regeneration that followed resulted in relatively extensive areas of even-aged western redcedar stands with a minor component of Douglas-fir and western hemlock. Natural regeneration of a large component of western redcedar after fire is unusual for coastal British Columbia where post-fire regeneration includes primarily Douglas-fir and/or western hemlock.

Sampling and Statistical Analyses

The population sampled consists of all naturally established, unmanaged, immature, even-aged stands with western redcedar as a dominant species which are accessible (500 m on each side of access roads with a 20 m buffer strip adjacent to roads). Potential candidate stands were previously identified by an established map for the drier area (Klinka and Krajina 1986) or by a pre-sample reconnaissance for the wetter area. The study stands ranged widely in age (Table 1) and were uniformly stocked with a relatively uniform, single tree layer which featured dominants of one or both study species. In order to avoid observer bias in choosing sample plots, we walked through the candidate stands, and the first plot meeting the criteria for site index determination (relatively uniform in soil, understory vegetation, and tree layer characters, uniformly stocked without a history of damage or suppression) was chosen for sampling. Results thus apply to the population of all plots meeting the criteria for site index with western redcedar as the dominant species within 500 m of either side of access roads in these two particular areas.

TABLE 1. Range and mean of stand age at breast height (years) and site index (m at 50 years breast height age) of the study stands.

Species Characteristic	Range		Mean
Western redcedar		(n = 105)	
Stand age (years)	37-88		56
Site index (m @ 50 years b.h. age)	13.0-33.8		25.8
Western hemlock		(n = 63)	
Stand age (years)	40-112		56
Site index (m @ 50 years b.h. age)	19.1-36.5		28.8

One hundred and five sample plots 0.04 ha in area (20 m x 20 m) were established in the candidate stands; 42 plots had western redcedar only and 63 plots had in addition to western redcedar a component of western hemlock suitable for site index estimates. The distribution and sample size of the plots is given in Table 2. Topography, understory vegetation, and soils of each sample plot were described using the site diagnosis procedure outlined in Green and Klinka (1994). Sites were identified to one of seven soil moisture regimes (SMR) – classes framed along a soil moisture gradient ranging from sites having a prolonged water deficit (very dry) to sites having no water deficit (fresh) to sites having a water excess (wet) – and one of five soil nutrient regimes (SNR) – classes framed along a soil nutrient gradient ranging from sites having low amounts of available nitrogen (very poor) to sites having high amounts

TABLE 2. Distribution and sample size of study stands by species and biogeoclimatic subzone.

Species	Subzone CWHdm	CWHvm	Total
Western redcedar	35	70	105
Western hemlock	19	44	63

of available nitrogen (very rich). The combination of SMR and SNR forms a cell on an edatopic grid (see Table 3 for an example). Identification of SMR and SNR was based on a heuristic synthesis of topographic and soil morphological properties, augmented by indicator plant analysis (Klinka et al. 1989).

In each sample plot, the five largest diameter trees of each of the study species with no obvious evidence of growth abnormalities and damage were measured for age at breast height, using an increment borer, and height, using a clinometer. Site index was taken from height growth tables of Kuruc[1] reported in Mitchell and Polsson (1988) for western redcedar and Wiley (1978) for western hemlock.

For western redcedar, the mean, 95% confidence intervals for the mean, standard deviation, and 95% confidence intervals for the standard deviation (using a χ^2 statistic) were calculated for each subzone and each combination of the SMR and SNR, and summarized on an edatopic grid. For comparison of the two subzones, the mean site index of the plots having the same SMR/SNR combinations were tested for differences using a *t*-test. A comparison of site index between western redcedar and western hemlock utilized the subset of 63 plots where both species were measured on the same plot. The Pearson correlation was used to relate the site index of the two species and a paired comparison *t*-test was used to test for differences between the means. The difference in site index of each species on the same plot was calculated and summarized.

Results

In both subzones, the maximum site index occurred on sites identified by field procedures as having no moisture deficit or excess and high nitrogen availability (moist/rich sites). Site index decreased on sites identified as having (1) either an inferred moisture deficit (very, moderately, or slightly dry SMR) or moisture excess (very moist, wet, and very wet SMR), and (2) inferred less nitrogen availability (very poor, poor, medium SNR) (Tables 3 and 4). The estimated population variation in site index associated with various combinations of SMRs and SNRs indicated that although the estimated standard deviation was small, the confidence intervals were large for most cells on the edatopic grid. The mean site index was significantly greater ($p < 0.05$) in the CWHdm subzone compared to the CWHvm subzone on most sites with the same SMR/SNR combination (slightly dry/medium, fresh/medium, moist/medium, moist/rich). Significant differences were not detected on the very moist/rich combination.

Comparisons of the site index of western redcedar and western hemlock growing on the same plot showed: (1) the Pearson correlation coefficient was 0.82; (2) the mean site index for western redcedar was 26.3 m and for western hemlock 28.8 m, and the means were significantly different ($p < 0.001$); and (3) on only one of the 63 plots the site index of the two species was the same, and on only seven of the plots the site index of western redcedar was greater than western hemlock (Figure 1).

Discussion

Due to a small sample size, the results reported here should be considered as preliminary until a larger data base is collected. However, in the meantime until such a data base is generated, operational needs must be addressed. Thus for operational use we present estimates of mean and standard deviation, and respective 95% confidence intervals of measured site index for various combinations of SMR and SNR for two subzones (Tables 3 and 4). For preliminary use in areas south and north of the vicinity of Vancouver, users should consider the influence of even a small difference in climate on the site index of western redcedar growing on the same soil conditions. Therefore, on similar soil conditions site index of western redcedar may be higher in the southern portion of its range in the United States and considerably lower in north coastal B.C. and southeastern Alaska.

A larger sample size is necessary in some cases to gain a more precise estimate of the population mean, and in most cases to gain a more precise estimate of the population standard deviation. However, extensive even-aged stands of western redcedar are rare in British Columbia. Where the sample size is five or greater, the mean estimates are relatively precise, the mean confidence intervals being generally less than one meter, with a few exceptions. However, for sample sizes less than five there is a dramatic loss of precision with relatively large confidence intervals. Although estimates of the population standard deviation were

Actual soil moisture regime	Soil nutrient regime				
	very poor	poor	medium	rich	very rich
very dry	13.4±5.4 0.6 0.3 – 19.1 n = 2				
moderately dry		22.2±7.2 0.8 0.4 – 25.5 n = 2			
slightly dry		24.4±0.6 0.5 0.3 – 1.4 n = 5	26.7±1.4 0.9 0.5 – 3.4 n = 4		
fresh			29.7±0.8 1.0 0.7 – 1.9 n = 9		
moist			30.3±2.7 1.1 0.6 – 6.9 n = 3	32.2±3.5 1.4 0.7 – 8.8 n = 3	29.0 n = 1
very moist				29.1±1.5 0.6 0.3 – 3.8 n = 3	32.0 n = 1
wet			16.5 n = 1	25.4 n = 1	

TABLE 3. Mean site index (m @ 50 years breast height age), ±95% confidence interval (m), standard deviation (m), 95% confidence interval for the standard deviation (m), and sample size for each combination of SMR and SNR for western redcedar in the dry maritime Coastal Western Hemlock (CWHdm) subzone.

Actual soil moisture regime	Soil nutrient regime				
	very poor	poor	medium	rich	very rich
very dry					
moderately dry					
slightly dry		20.9 n = 1	22.0±6.3 0.7 0.3 – 22.3 n = 2	24.8±0.5 0.2 0.1 – 1.3 n = 3	
fresh		23.0±0.6 0.5 0.3 – 1.4 n = 5	24.7±0.8 0.8 0.5 – 2.0 n = 6	26.2±0.7 0.8 0.5 – 1.8 n = 7	
moist			26.3±0.6 0.5 0.3 – 1.4 n = 5	28.3±0.5 1.0 0.7 – 1.5 n = 16	
very moist		21.8 n = 1	25.2 n = 1	27.9±1.6 1.7 1.1 – 3.7 n = 7	27.5±0.6 0.5 0.3 – 1.4 n = 5
wet			17.8±1.9 2.1 1.4 – 4.6 n = 7	22.5±0.5 0.2 0.1 – 1.3 n = 3	26.2 n = 1

TABLE 4. Mean site index (m @ 50 years breast height age), ±95% confidence interval (m), standard deviation (m), 95% confidence interval for the standard deviation (m), and sample size for each combination of SMR and SNR for western redcedar sampled in the very wet maritime Coastal Western Hemlock (CWHvm) subzone.

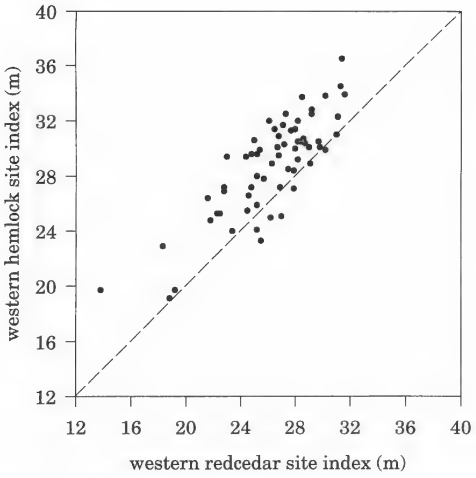

Figure 1. Site index comparisons between western redcedar and western hemlock (n = 63). The dashed line represents a line of equal site index.

generally less than 1.5 m, and all less than 2.0 m (Tables 3 and 4), the upper confidence interval showed that the population variation could be much more, and again especially where the sample size is less than five. At present if users wish to know the consistency of the estimate of site index on an individual site basis, the upper confidence value on the estimate of the population standard deviation may make such an inquiry less reliable.

A shortfall of this study lies in the identification of SMR and SNR from field measurable properties rather than directly with soil chemical measures. However, during the development and refinement of the edatopic grid concept, SNR classes were derived from actual soil chemical measures (Courtin et al. 1984; Kabzems and Klinka 1987; Klinka and Carter 1990), and SMR classes were derived from a water balance model (Klinka and Carter 1990; Wang and Klinka 1996). Further, Klinka et al. (1994) have demonstrated a relationship between the field-derived SNRs with measures of soil nitrogen in the central interior of British Columbia.

For forest management scenarios where timber production is the primary objective, practitioners may consider that the site index of western redcedar was consistently less than western hemlock for western redcedar values from 13.8 to 31.6 m. However, unlike intraspecific comparisons of site index, interspecific comparisons can not be extrapolated to comparisons of productivity. The values are to be used in a growth and yield model to generate comparative productivity between the two species. The consistently lower site index for western redcedar compared to western hemlock differs from that of the Queen Charlotte Islands in B.C. (53°N latitude), where Green (1989) found the site index of western redcedar to be greater than western hemlock at site index values between 11 and 19 m, and the same between 19 and 24 m. Based on this northward trend, we may predict that in southeastern Alaska the site index values will be larger for western redcedar over western hemlock, while in Washington and Oregon the site index of western hemlock will be larger than western redcedar by an amount even greater than reported here.

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Effects of Multiple Fires on the Structure of Southwestern Washington Forests

Abstract

Fire frequency, intensity, and size can influence the nature of forest development, with potentially profound effects on ecosystem processes and the abundance of native species. The effect of an intense wildfire and subsequent severe fires within a short period (reburns) on forest establishment, composition, and structure was examined in the 16,000 ha Siouxon Creek watershed in the western Cascades of southern Washington. Evidence of large intense fires and small patchy fires was found in the watershed, with 4 fires occurring since 1900. Tree establishment was rapid and abundant throughout most of the area burned in the 1902 fire, possibly from survival of on-site seed sources. Tree establishment was delayed on most reburns and corresponded with years of abundant regional Douglas-fir (*Pseudotsuga menziesii*) cone production, indicating off-site sources of seed. Western hemlock (*Tsuga heterophylla*) was less abundant on reburns than on the 1902 burn. The ranges of Douglas-fir ages within stands were greater on reburns than on single burns, but fire frequency effects could not be distinguished from potential stand age and composition effects. There were no clear patterns of tree species abundance related to presumed dispersal distances of up to 3 km from unburned forest. Fire frequency, topography, and seed source had important effects on forest structure and composition across the watershed.

Introduction

Wildfire is the primary natural disturbance in the forests of the Cascade Range (Munger 1930, Franklin and Hemstrom 1981), but little is known about the effect of fire frequency on forest composition and structure. Understanding the role of fire in forest development is crucial if we wish to maintain native species and ecosystem processes (Hansen et al. 1991). Although fire on the west side of the Cascade Range is usually described as infrequent and catastrophic, many large burns experienced repeated high-intensity fires ("reburns") within decades of the initial catastrophic fire (Agee 1993). Compared to forest development after single intense fire events, tree establishment on reburns is often sparse or nonexistent for decades after the last fire (Hofmann 1917, Isaac and Meagher 1936, Larsen 1925). It is unknown whether poor dispersal of tree seeds into large burns, poor tree regeneration caused by degraded soil properties, or some other factor are causes of slow forest development on reburns. Reburn fires can be more intense, and therefore may have greater effects, than the original burns in Douglas-fir forests because recently-burned forests often have greater amounts of fuel than mature forests (Agee and Huff 1987). Indeed, repeated wildfire has been hypothesized as a factor causing slow establishment of many of the old-growth forests in the Cascades that originated around 500 years ago (Franklin and Hemstrom 1981).

The size and shape of fires, and the composition of surrounding forests, may have important effects on forest development within large burns. Seed dispersal typically declines with distance from seed-bearing adults, but dispersal curves vary dramatically among species (Harper 1977), potentially influencing forest composition at large spatial scales. Although the density of natural tree regeneration on clear-cuts in the Cascades declines predictably with distance from the forest edge (Isaac 1943), some studies have found copious regeneration many kilometers from the edges of large burns (Hofmann 1917, Isaac and Meagher 1936).

The purpose of this study was to characterize 1) the fire history of a watershed in which multiple fire events were known to have occurred and 2) compare the age structure, size structure, and tree composition on sites that experienced a single severe fire in 1902 ("single burn" sites) with sites that burned in 1902 and in subsequent severe fires within 30 years of the 1902 fire ("reburn" sites). The focus of the study was on the Siouxon Creek watershed of southern Washington.

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Methods

Study Area Description

The Siouxon watershed is located on the west side of the southern Cascade Range of Washington, centered at 122°15'W latitude and 46°00'N longitude, about 24 km south of Mt. St. Helens. The study area of 16,000 hectares included most of the Siouxon Creek and North Siouxon Creek drainages and portions of the North Fork of the Lewis River drainage (currently Yale Reservoir) across from the town of Yale, WA. Both Siouxon creeks drain to the west into Yale Reservoir. Topography is moderately steep and dissected, with elevations ranging from 149 m at the surface of Yale Reservoir to 1271 m at the summit of Siouxon Peak. Glacial tills are found in the main Siouxon drainages and at the heads of many Siouxon tributaries (Mundorff 1984). The moist temperate climate is characterized by generally mild wet winters and warm dry summers. Annual precipitation near the town of Cougar averages 292 cm (National Climatic Center 1932-87), with a continuous winter snowpack forming above about 1000 m (Topik et al. 1986).

Vegetation in the study area falls into two zones. The *Tsuga heterophylla* Zone, dominated by Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), occurs below about 1000 m. The *Abies amabilis* Zone, dominated by Pacific silver fir (*Abies amabilis* Dougl. Forbes) and noble fir (*Abies procera* Rehder), occurs above 1000 m (Topik et al. 1986). The bulk of the study area had seen little forest management activity.

Fire History

The fire history of the study area was reconstructed using historical forest-type maps, written accounts, aerial and panoramic photographs, and field samples of dominant tree ages. The objective was to identify the boundaries of, and tree ages within, fires occurring since 1900. Forest-type maps of Washington made early in the century (Plummer et al. 1902, USDA 1936) and fire atlases (USDA Forest Service n.d.—no date—1) were useful starting points. Aerial photos from 1959, 1976, and 1984 and panoramic photos taken from lookout stations in the early 1930s (USDA Forest Service n.d. 2) were studied for evidence of large remnant trees, tree seedlings and saplings, and edges between forests with different tree sizes. Features were drawn onto a base map, using visible landmarks in the photos to match those on topographic maps.

Ages of dominant trees from plots (described below) and point samples were used to date the most recent fire (after Hemstrom and Franklin 1982, Agee 1993); tree stems, increment cores, and stumps were carefully examined for post-establishment fire scars. Forty-six "reconnaissance" points were located in areas where fire boundaries on air photos were unclear; recently logged sites were preferentially examined. Three or more dominant trees or large stumps at each reconnaissance point were aged by counting rings on increment cores or on stump surfaces scraped clean with a pocket knife. Rings on young trees were distinguishable and readily counted in the field, otherwise cores were collected for later analysis. Clear-cutting dates were known in most cases from direct observation, or were estimated from the annual height increment of planted trees.

The age of the oldest tree at a sample point was considered to date the origin of the stand. Stands which established within eight years of each other and were contained within fire boundaries identified in historical documents and photos were interpreted as being cohorts following a common fire. The eight year criterion was chosen to accommodate estimated errors in aging stands (Gray 1990). Stand ages, stand boundaries visible in aerial and lookout photographs, and fire dates from historical sources were combined to produce a single map of the burns in the study area (see Gray 1990 for mapping details).

Stand Structure

Forest structure data was collected in 1988-9 in two different ways: "survey" plots were placed throughout the study area to sample stand types and ages, and paired "detail" plots were placed on areas of adjacent single and multiple burns. Fifty survey plots were distributed over five elevation zones and two general aspects (north and south) to match the relative area of those zones and aspects in the study area (Gray 1990). Some areas far from roads and trails were under-sampled. Plots were located in stands with a concentration of conifers, which excluded most riparian areas. Survey plots were circular with an area of 250 m^2 (8.9 m radius). Within each plot, diameter at

breast height (DBH, at 1.38 m) was measured on all live trees greater than 5 cm DBH and tree height was measured on the largest tree using tape and clinometer. Increment cores were taken from three large early-seral trees (usually Douglas-fir). The presence of charred snags and logs on a site proved to be a reliable indicator of a reburn (Klopsch 1985). They are created by burning of trees which died and shed their bark after the first fire. While some of the large snags in single- burn areas were charred, almost every large snag in multiple-burn areas was heavily charred.

Seven pairs of detail plots were established on sites dominated by Douglas-fir, with one of each pair located in an area burned in 1902 ("single burn"), and the other located in an area burned in 1902 and burned again within 30 yrs ("reburn"). The plots in a pair had similar elevation, aspect, slope, topography, soil type, and plant association (Gray 1990). The environmental conditions sampled by these paired plots ranged from moist low elevation flat sites to drier, moderate elevation steep sites. Pairs were designated by letter (A-G) and plots within a pair differentiated by number (e.g. A1 and A2 are paired single burn and reburn plots, respectively). Tree DBH was measured on all standing live and dead trees taller than breast height (1.38 m) in circular 250 m^2 plots around each detail plot center. Ages were determined for up to 25 Douglas-fir trees within a 500 m^2 circular plot around each detail plot center; trees were randomly selected if more than 25 Douglas-fir were present. Increment corings of selected trees were taken up to three times in an attempt to hit the pith of each tree. Heights of three cored large-diameter trees were measured. Increment cores were also taken on up to five trees of each of the other species present over the range of tree sizes present.

Data Analysis

Tree age (since seed germination) was estimated from stump and increment core samples by the following methods (see Gray 1990 for details). Collected increment cores were mounted in wood blocks and sanded and rings were counted with a hand lens or dissecting microscope. For those cores that did not intersect the pith of the tree, the curvature of the innermost rings on the cores was used to estimate years to the pith (Arno and Sneck 1977). Of 143 cored trees on survey plots, 38% hit the pith and 44% were estimated to have missed the pith by 3 years or less. Of 264 trees cored on detail plots, 49% hit the pith and 42% were estimated to have missed the pith by 3 years or less. Age estimates for 11 very large trees found on moist, sheltered sites which could not be cored near to the pith were developed by calculating the inner diameter which had not been cored and the age at which the average Douglas-fir in a productive (site class I) stand would reach that breast-height diameter (McArdle and Meyer 1930).

Estimates of the time it took for sampled trees to grow from germinants to the height at which increment cores were taken or stumps were cut (mean height of 47 cm for all samples) were developed using information on Douglas-fir seedling height growth as a function of site class (McArdle and Meyer 1930). Site class and site index are measures of an area's growth potential for trees, and were derived for the plots in this study using tree height and breast-height tree age (King 1966); reconnaissance sites were assumed to be of intermediate site class III, the median for the study area. The same seedling growth relationship was used for western hemlock, Pacific silver fir, and noble fir trees, since little detailed information on height growth below breast height exists for these species (Hanzlik 1925 and Williams 1968 did find similar early height growth for open grown noble fir, silver fir, hemlock, and Douglas-fir). All red alder (*Alnus rubra* Bong.) and bigleaf maple (*Acer macrophyllum* Pursh.) were assumed to be 2 yrs old at core height based on personal observations of early growth on disturbed mesic sites. Estimated errors for individual tree ages ranged from ±2-5 years, depending on method, sample height, and presence of the pith in the sample (Gray 1990).

Differences in the time required for Douglas-fir establishment between single burns and reburns was evaluated with an F-test on the within-stand variance in tree ages from detail plots. The effect of a range of environmental factors and indicators on tree species composition in survey and detail plots was analyzed for Douglas-fir and hemlock with stepwise multiple linear regression (Zar 1984). The proportion of total plot basal area for each species was regressed on elevation, slope, aspect (transformed to the cosine of aspect-45°), slope*aspect, stand age, the shortest distance from pre-1900 age stands (measured from the fire map),

and site index (from King 1966). Significance levels for inclusion of variables in the regression models were set at p=.15. Analyses of residuals (with proc univariate in SAS Institute 1987) indicated that proportional basal area data for Douglas-fir and western hemlock did not violate assumptions of homoscedasticity and normality (as is common when most data are between .30 and .70—Zar 1984). Proportional basal area data for other species appeared to violate these statistical assumptions, so the importance of the different site factors were tested individually on species presence using the non-parametric Wilcoxon-Mann-Whitney rank sums method (Zar 1984). Differences in species abundance between single burns and reburns was evaluated with a t-test on proportional basal area for Douglas-fir and western hemlock (because they were present on most plots) using the Satterwaithe approximation for unequal variances (SAS Institute 1987). Linear regressions of tree density per plot (log-transformed to normalize residuals) on distance from pre-1900 stands were also calculated for Douglas-fir and western hemlock.

Results

Fire History

Four separate, high intensity fires occurred in the Siouxon drainage in the 1900s and evidence of earlier fires was also apparent (Figure 1). Douglas-fir trees established within a few decades of 1480 in five stands and in the late 1500s and mid-1600s in five other stands throughout the study area. Three separate fire events around 1803, 1824, and 1848 may have preceded the establishment of stands in the southwest, west, and northwest portions the study area, respectively. Any fires which did occur in the early 1800s must have been relatively small, since observations indicated that most of the snags created by the 1902 fire were greater than 100 cm in diameter, which is larger than the size of the average 100 yr old Douglas-fir on even the best of sites (70 cm—McArdle and Meyer 1930). Thus most of the stands in the Siouxon drainage were probably old-growth forests over 300 years old when the fire of 1902 killed most of the trees in the drainage. The few trees which survived the 1902 fire and were still alive in 1959 (the date of the earliest air photos examined) were located along valley bottoms and headwalls (Figure 1). Historical maps, documents, photos, and stand ages concur that smaller intense fires occurred within the 1902 burn in 1919, 1927, and 1932. A 120 ha 1918 fire was mapped on Mt. Mitchell (USDA n.d. 1) but field evidence of it would have been destroyed in the subsequent 1919 and/or 1932 fires (the amount of overlap of these later events is not known).

Stand Structure

The timing of forest establishment after fire differed between single burns and reburns. Tree regeneration was prompt after the 1902 fire, with 51 of 59 survey and reconnaissance points within the 1902 burn dated between 1902 and 1909 (Figure 1), and regeneration on all 7 single burn detail plots dated between 1901 and 1906 (Figure 2). Tree regeneration was delayed up to 5 years on two of the three reburns, with most stands in the 1919 reburn initiating after 1923 and most stands on the 1927 reburn initiating after 1932 (Figures 1 and 2). Stands on the 1932 reburn apparently established within 1-2 years of the fire.

Douglas-fir on single-burn sites established over a shorter period of time than Douglas-fir on reburn sites, indicated by comparing the variance in tree ages on the detail plots ($F_{.05(1),139,111}$= 1.38, p= .042)(Figure 2). There was considerable variation in stand age structures within burns, however. Douglas-fir on wetter sites in the single burn (A1, B1, C1, and D1) apparently established more rapidly (over about 12 yrs) than Douglas-fir on drier sites in the single burn (24 yrs or more for E1, F1, and G1) (Figure 2). In addition, the largest western hemlock tended to establish sooner after fire on the wetter sites (A1 and A2) than on the drier sites (G1 and G2).

Western hemlock was less abundant (as a fraction of total stand basal area) in reburn stands than in single burn stands ($t_{.05(2),59}$=2.31, p= .0242), and tended to be more common in the largest diameter classes present in single burn stands (Figure 3). Douglas-fir, on the other hand, was more abundant in reburn stands than in single burn stands ($t_{.05(2),59}$= -4.36, p= .0001). The structure of most stands consisted of Douglas-fir clumped in the largest diameter classes and shade-tolerant western hemlock in a range of diameter classes, and standing dead stems in the smallest diameter classes (Figure 3). These characteristics indicate stand growth following catastrophic disturbance and self-thinning mortality of dense populations.

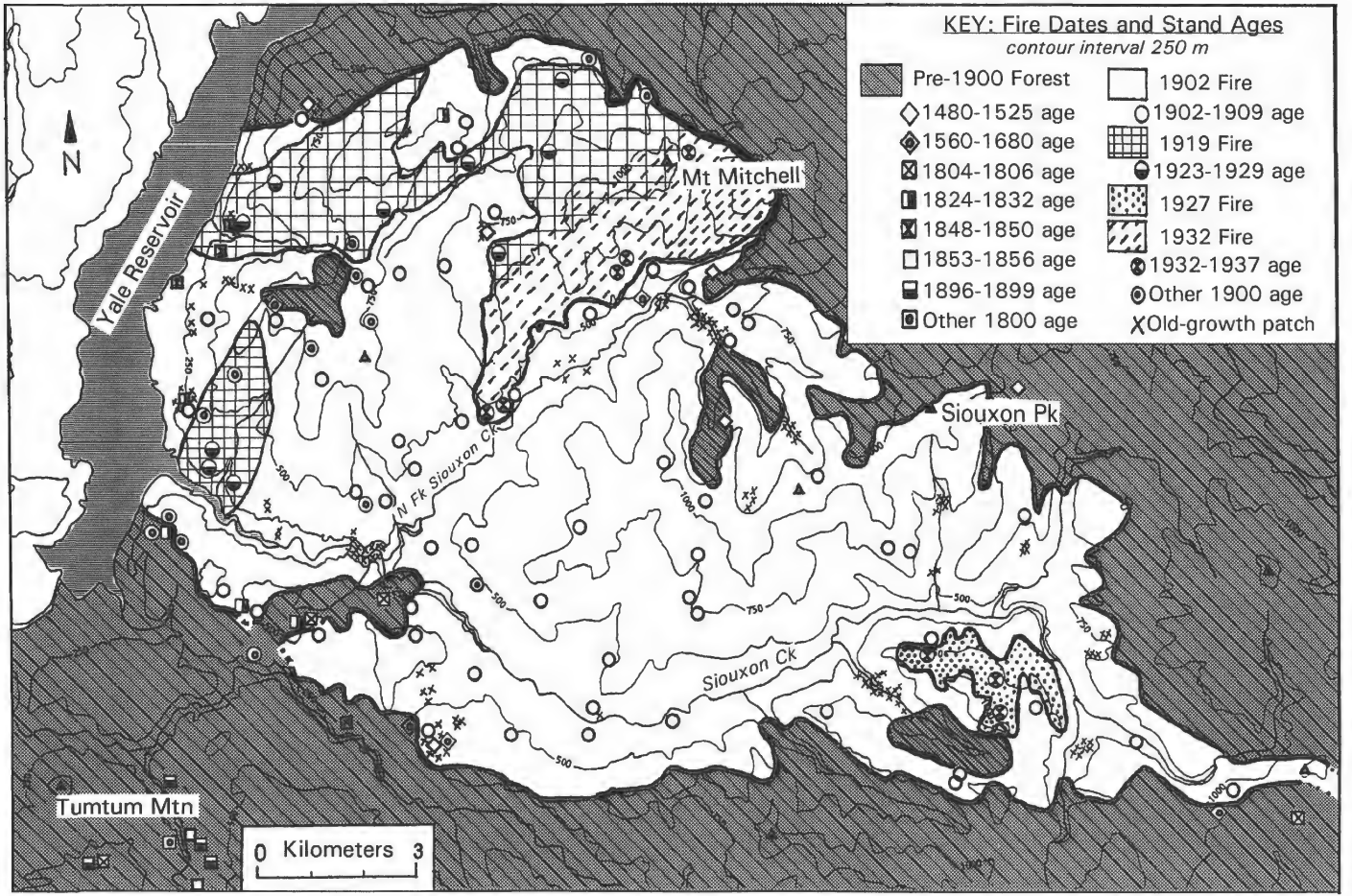

Figure 1. Map of fires occurring after 1900 and stand ages in the Siouxon drainage. The 1902 fire is unshaded, and the precise boundaries of the 1927 and 1932 reburns on Mt. Mitchell are unknown. Stand age symbol shapes vary among centuries: circles=1900s, squares=1800s, and diamonds=pre-1800.

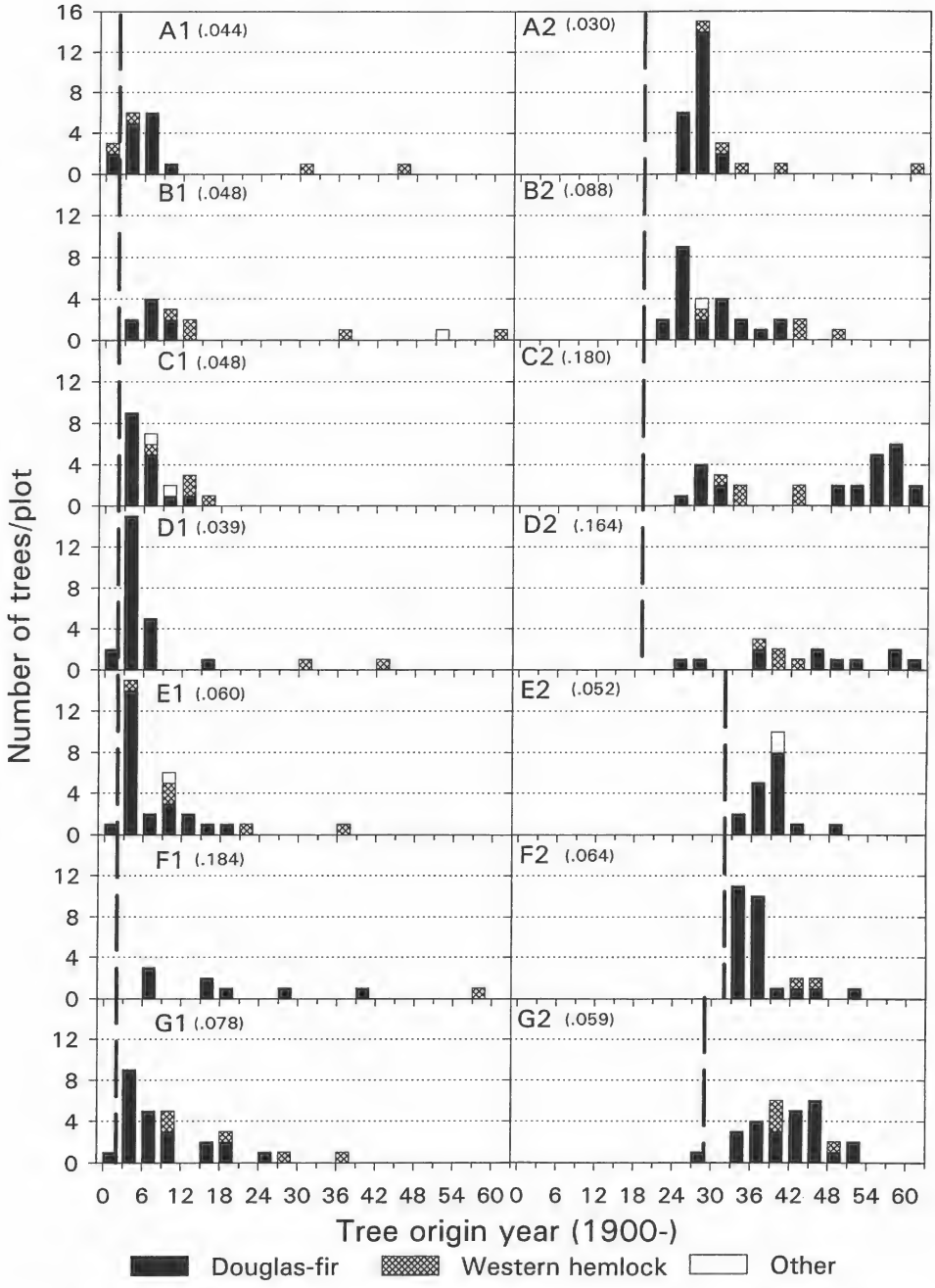

Figure 2. Estimated germination dates of Douglas-fir and selected individuals of other species on paired detail plots, showing variance in Douglas-fir age in parentheses and a dotted line indicating the year of the last fire for each plot. "Other" species include western redcedar, noble fir, and red alder.

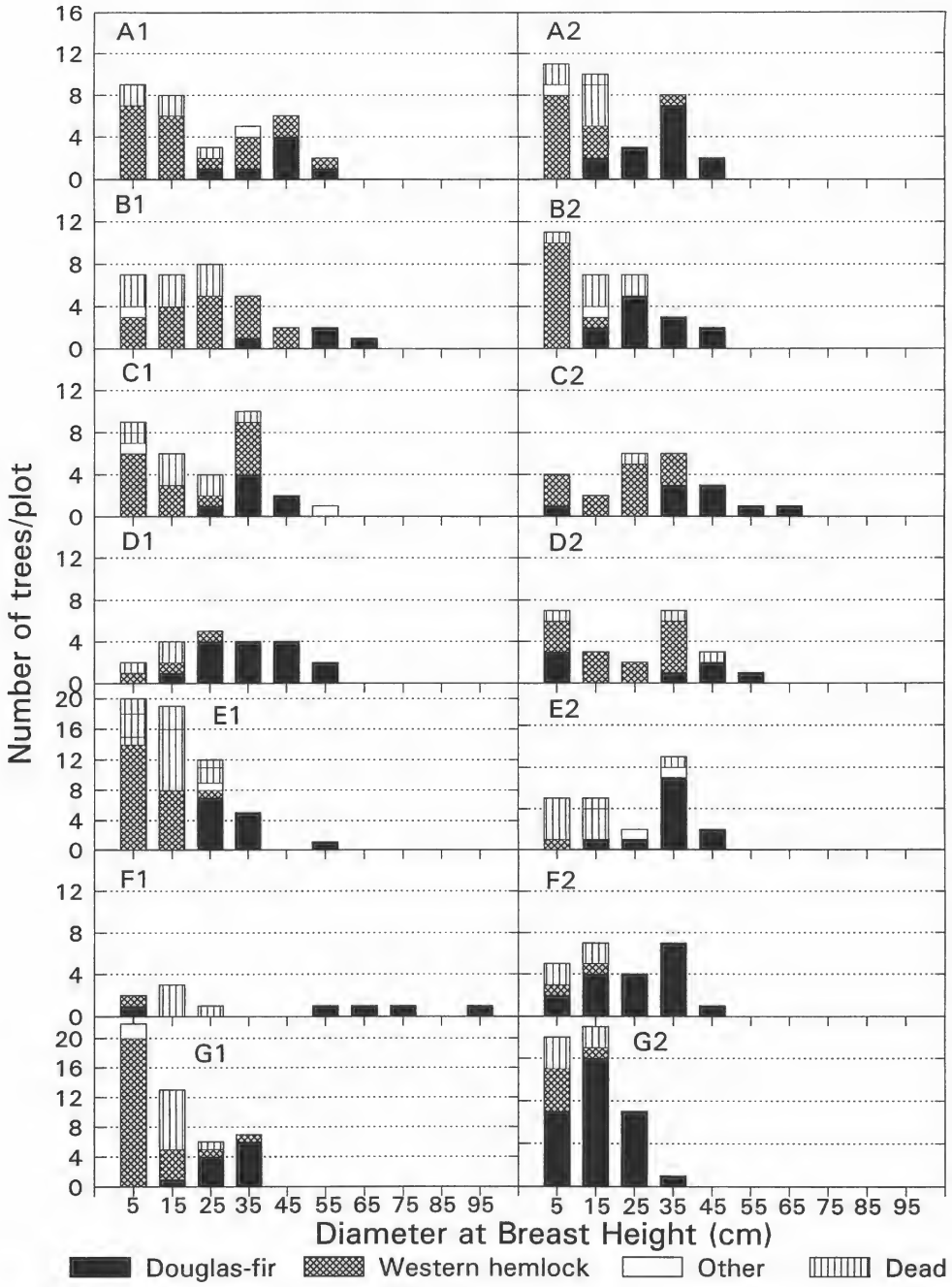

Figure 3. Diameter distributions of all species on paired detail plots (1/40 ha). "Other" includes western redcedar, Pacific silver fir, noble fir, and red alder; "dead" refers to standing dead stems of Douglas-fir, western hemlock, and red alder. Note change in scale for plots E1 and G1, but not for E2 or G2.

TABLE 1. Relationship between plot characteristics and species composition. Coefficients (ß) and p-values of significant factors selected by stepwise multiple linear regressions on proportional basal area are shown for Douglas-fir and hemlock. Rank-sum test Z and p values for individual factors are shown for presence of the other species. Number of plots (out of 61) with species present is shown under species name. Elev=elevation (m), age=stand age, dist=distance from pre-1900 stands, Site Ind=site index (King 1966).

Species		elev (m)	slope (%)	slope* aspect	stand age	dist (m)	Site Ind
Douglas-fir	ß:	-0.068	0.60		-0.74	0.0071	
n=57		(.0001)	(.0018)		(.0038)	(.0508)	
hemlock	ß:		-0.51	0.27	0.60		-0.28
n=56			(.0018)	(.0026)	(.0048)		(.0089)
silver fir	Z:	3.8				-2.0	-2.6
n=7		(.0001)				(.0437)	(.0086)
noble fir	Z:	3.5					-2.3
n=6		(.0004)					(.0227)
redcedar	Z:		-2.4		3.1		
n=19			(.0160)		(.0021)		
alder	Z:	-2.8		-2.6			
n=11		(.0052)		(.0094)			
bigleaf maple	Z:	-2.7				-2.0	2.4
n=8		(.0062)				(.0488)	(.0162)

The age and diameter structures of some stands differed substantially from those found in the majority of stands (Figures 2 and 3). Douglas-fir in single-burn detail plot F1 were relatively large, had established over a 34 year period, and were growing at low density in a relatively open stand. Slow establishment may have been a result of poor regeneration caused by summer drought on the coarse, cobbley substrate at this site, which apparently was an old glacial deposit (Mundorff 1984). Douglas-fir age and size distributions in reburn plot C2 suggest two distinct cohorts of trees, which appeared to be spatially distinct. Periodic, semi-continuous establishment of fire-sensitive hemlock in this stand suggests that the young Douglas-fir saplings did not establish following a second disturbance; instead, they may have established in gaps in the dense, mature stands of brush which occupied parts of this site. The broad age and size distribution of Douglas-fir on reburn plot D2 may be related to the mortality of the larger-diameter trees (Figure 3), which may have maintained sufficient light levels in the stand for survival of the smaller, younger Douglas-fir. Large basal scars oriented in various directions were found on many of the larger live and dead trees in this stand, suggestive of feeding by bear or porcupine (fire scars usually face in the same uphill direction—Brown and Davis 1973).

The presence and abundance of several tree species were significantly related to one or more environmental factors that were sampled by the distribution of survey and detail plots across the watershed (Table 1). The multiple linear regression for Douglas-fir (r^2=.48) indicated greater abundance on sites at lower elevations, on steeper slopes, in younger stands, and at greater distances from old-growth stands. The regression model for western hemlock (r^2=.37) indicates greater abundance on gentle, north-facing slopes, older stands, and sites of relatively low productivity for Douglas-fir (low site index). Both Pacific silver fir and noble fir were found primarily at higher elevations, which also tended to be sites with lower site indices. Pacific silver fir was also associated with sites that were relatively close to old-growth stands. Western redcedar (*Thuja plicata* Donn.) tended to be present on flatter slopes and in older stands. Red alder tended to occur on steeper, south-facing low elevation sites, while big-leaf maple

tended to occur on productive, low elevation sites that were relatively close to old-growth stands. Distance from old-growth stands was at best only a marginally significant factor for species' proportional basal area or presence (Table 1). Tree density was weakly related to distance from old-growth for both Douglas-fir and western hemlock (r^2 =.005 and .074 and p = .60 and .086, respectively).

Discussion

Fire history

Evidence of both large intense and small patchy fires was found in the Siouxon Creek watershed. The oldest Douglas-fir occurred throughout the study area and were established around 1500 A.D., which is approximately when most remaining old-growth stands in the Washington and northern Oregon Cascades became established (1450-1550 A.D.—Franklin and Hemstrom 1981, Agee 1993), suggesting widespread and/or recurrent fire at that time. The relatively small fires that may have occurred at the western end of the study area in the early 1800s could reflect localized ignitions by humans. The Cowlitz tribe inhabited the Lewis River valley (Ray 1974) and maintained prairies by regular burning (Leopold 1987); one of these prairies (known as Chelatchie Prairie) is located only 5 km southwest of the study area and is clearly depicted in Plummer et al.'s (1902) historical map. Ignition by European trappers and explorers, which were travelling through southern Washington by the 1820s, is also possible, however. The large 1902 fire was simultaneous with many intense human-caused fires which burned in western Oregon and Washington in September 1902 (Oregonian 20/9/02, Holbrook 1943). The few trees surviving the 1902 fire in the Siouxon were only found in clumps in sheltered valleys or individually along creeks. The cause of the more recent fires in the Siouxon is unknown; although of catastrophic intensity, they were significantly smaller than the 1902 burn. In summary, it appears that most of the study area consisted of mature and old-growth forest that burned intensely in 1902, portions of which burned once again in smaller high-intensity fires. An undefined area around Mt. Mitchell may have burned two or three times since the 1902 burn, and the western edge of the study area may have experienced multiple patchy burns in the early 1800s.

Some of the fire events examined in this study correspond well with the infrequent, high-intensity fire cycles described for moist Douglas-fir forests, in which fire intervals exceed 200 years and regenerating forests are even-aged (Hemstrom and Franklin 1982, Agee 1993). Considerable variation in fire frequency and intensity can occur within an area, however (e.g. Yamaguchi 1986, Morrison and Swanson 1990), thus the range of fire size and frequency found in the Siouxon may be representative of many areas in western Washington.

Stand Structure

Douglas-fir trees on single burn sites established over a shorter period of time than Douglas-fir trees on sites that burned again within 30 years (reburns), but the difference was not dramatic and therefore may have been caused by differences in stand development rather than effects of fire frequency on tree regeneration. Because single burn stands were older than reburn stands, the narrower age distributions in the older stands may have been caused by longer periods of self-thinning, in which the youngest, smallest individuals in a population die as dominant individuals develop (Harper 1977). Differences in animal-caused mortality or soil composition may also have contributed to the evident difference in age distributions between single burn and reburn sites. The apparently smaller range in tree ages on moist sites compared to drier sites may also have been due to site differences as opposed to differences in regeneration, because the intensity of thinning mortality increases with site productivity (Harper 1977).

Speed of establishment and within-stand density of Douglas-fir was not affected by distances of over three kilometers from unburned stands. Since Douglas-fir seed dispersal and regeneration declines to very low levels within 800 m of seed-bearing trees (Isaac 1930, Isaac 1943), seed sources must have been readily available after the 1902 Siouxon burn. Seeds can survive in green cones on trees that are killed by fire (Hofmann 1924, Isaac 1943); the 1902 fire occurred in mid-September, just prior to the onset of Douglas-fir seed dispersal (Reukema 1982). Seed production by Douglas-fir is irregular, however; whether seed was abundant in 1902 is not known. Alternatively, mature trees may survive catastrophic fires for a few years before succumbing to fire

injuries or outbreaks of Douglas-fir bark beetle (*Dendroctonus pseudotsugae*) which breed in the forest of fresh snags (Isaac and Meagher 1936, Agee and Huff 1987). Survival for only two years after fire would be sufficient time for a large "stress crop" of Douglas-fir seeds (Allen and Owens 1972).

The delay in establishment after fire for Douglas-fir on at least two of the reburns suggests a lack of on-site seed sources. Stands on the 1919 and 1927 burns established after 1923 and 1934, respectively, which were the first years of abundant regional Douglas-fir seed crops after each fire (Isaac 1943). Potential on-site seed sources may have been destroyed by the reburns, which may have been more intense than the 1902 burn because of greater amounts of fuel in the form of deep litter and understory plants (Agee and Huff 1987) and dense canopies of young trees close to ground fuels, which make intense crown fire highly likely (VanWagner 1977). Seed trees which survived the 1933 Tillamook fire were killed by subsequent reburns (Andrews 1944), and the same apparently happened on the Siouxon burn.

Despite the delay in establishment and the apparent lack of on-site seed sources, the rapid establishment of Douglas-fir on reburn sites indicates that regeneration was not impeded. Although most reburn sites were over 1 km from pre-1900 forest, all were within 600 m of extensive post-1902 stands. Dispersal from the large number of trees in the 1902 forest may have compensated for the light cone production characteristic of young trees. Herbs and shrubs apparently did not develop sufficiently on most reburn sites to compete with seedlings germinating 3-4 yrs after fire, possibly because vegetation recovery is often slow after intense fires (Halpern 1989, Dyrness 1973).

The density of western hemlock was not greatly affected by distances of over three kilometers from unburned stands, but it is unlikely that there were abundant sources of on-site seed after the 1902 fire. The small cones of western hemlock are probably less heat-resistant than those of Douglas-fir, and hemlock trees are much less fire-resistant than Douglas-fir (Minore 1979), so it is doubtful that hemlock seed survived the 1902 fire or was produced within the burn after the fire. However, hemlock seed can disperse much further than Douglas-fir (Isaac 1930), and its shade-tolerance (Minore 1979) allows it to establish in existing forests. Thus hemlock in the 1902 burn may have established from seed which dispersed from the edges of the burn over many years. Since seed dispersal was apparently not limiting, the reduced abundance of western hemlock on single burn sites compared to reburn sites could be attributed to soil degradation by repeated fire. The repeated intense fires on the reburn sites probably reduced soil organic matter and coarse woody debris to a much greater extent than the isolated fire on the single burn sites. Woody debris and soil organic matter represent important reservoirs of moisture (Harmon et al. 1986, Kimmins 1987) which are important to drought-intolerant hemlock during the summer drought of Cascade Douglas-fir forests (Gray 1995). For most species in this study, however, topography appeared to be of greater importance than fire frequency or distance from potential seed source.

The speed and density with which the forest established on both single burn and reburn sites in the Siouxon suggests that mesic Douglas-fir forests are quite resilient with respect to intense natural disturbances. This is in contrast to regeneration problems reported on the larger Tillamook and Yacolt reburns (Andrews 1944, personal observation) and on large clearcuts (Isaac 1943). The adequate stocking of stands in the Siouxon seems attributable to on-site seed sources after the 1902 burn, which are not present on large clearcuts, and proximal seed sources for reburns, which would not be the case after large fires. Poor tree establishment may also occur after greater fire frequency than was found in the Siouxon; many areas on the Yacolt and Tillamook burns experienced intense fire 3-5 times within 30 years (Felt 1977). Despite adequate forest establishment, less frequent reburning may have important effects on forest composition, as was detected for hemlock in this study. Future studies of reburns might focus on soil characteristics important to plant composition, since fire can reduce soil organic matter, decrease porosity, destroy mineral soil structure, and increase susceptibility to soil erosion (Swanson 1981). Loss of decaying wood in the soil, which is important for growth of mycorrhizal-forming fungi and nitrogen-fixing soil microbes may be a limiting factor to tree regeneration on reburns (Barrett 1982).

Understanding the nature and rate of forest development after large, intense forest fires has

important implications for forest ecosystems in the region. Most naturally-established Douglas-fir forests in the western Cascades developed after large, intense forest fires, many of which burned several times over a few decades (Agee 1993). The results of this study suggest that the size, intensity, and frequency of these past fires affected forest development and composition. Current forest management, however, tends to be patterned on simple models of stand development occurring after a limited range of disturbance types, and may not sustain the species adapted to more complex natural habitats (Hansen et al. 1991).

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Commercial Moss Harvest in Northwestern Oregon: Describing the Epiphyte Communities

Abstract

This paper describes the epiphytes impacted by commercial moss harvest in northwestern Oregon. Commercially harvestable epiphytes were sampled on hardwood tree trunks and shrub stems from 10 sites in each of the Cascade and Coast Ranges. Fifty species of mosses, hepatics, lichens, and vascular plants were found in over 500 epiphyte mats. Seven taxa were defined as "target" species, due to high frequency of occurrence and abundance. Six species were defined as "incidental" due to lower frequency and biomass but a high association with target species. The remaining 37 species were defined as "nontarget" species that would generally be avoided by commercial harvesters, but are often accidentally harvested. In the Cascade Range, *Neckera douglasii* was the most abundant harvestable epiphyte, with an average of 170 kg/ha of dry-weight harvestable material across ten sites. In the Coast Range, *Isothecium myosuroides* was most abundant, with an average of 530 kg/ha of dry-weight harvestable material. All harvestable epiphytes were less abundant in stands with high conifer basal area. Target species were most abundant in stands with relatively high hardwood basal area, except *Antitrichia curtipendula* which was most abundant in younger stands. Some nontarget and incidental species were also most abundant on tree trunks. To protect rare species and epiphyte diversity, moss harvest should be directed away from older forests with mature hardwoods and toward younger, mixed forests. Moss harvest should be prohibited in areas being managed toward "old growth" conditions to facilitate the development of complex epiphyte communities requiring substrate continuity.

Introduction

Epiphytes are a significant and diverse component of forests in the Pacific Northwest. Many species are old growth associates and are sparse to absent in young and mature forests (Lesica et al. 1991, Neitlich 1993). Epiphytes play a variety of roles in forest ecosystems, from nesting material for birds (FEMAT 1993) and habitat for invertebrates (Peck and Moldenke in prep.) to nutrient sinks (Brown and Bates 1990). Epiphytes are increasingly being removed from the forest to feed a growing floral and craft trade (Howell 1991, Johnson 1992, Peck 1990), yet little is known about the ecological impact of this harvest. Estimates based on permits for moss harvest on publicly owned lands put the total legal moss harvest in northwest Oregon at more than 226,800 kg/year (500,000 lb/year; moisture content between 10 and 18%). The illegal harvest is thought to be at least twice the legal harvest.

The current study comes at a time when forest managers are required to protect rare epiphytes (ROD 1994) and manage moss harvest for sustainability (USDA Forest Service 1995). Baseline data for management have been lacking, prompting the current study to address these basic questions about commercial moss harvest:

(1) What do commercial harvesters consider to be a "commercially harvestable moss mat"?

(2) What species of epiphytes compose these mats?

  (a) How many species are affected by harvest?

  (b) Are species targeted for harvest quantitatively distinct from species that are not targeted?

(3) Do target and nontarget species differ in their patterns of abundance on the landscape?

This kind of basic information about commercially harvestable moss will enable managers to begin to assess the probable impacts of commercial moss harvest on sustainability and species of concern (e.g., species listed under the "Record of Decision for Amendments to Forest Service and Bureau of Land Management Planning Documents Within the Range of the Northern Spotted Owl" (ROD 1994). This information will also provide a starting point for future investigations of harvestable moss inventories, regrowth rates, and the impacts of harvest on the communities and ecosystem functions of epiphytic bryophytes.

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Methods

Sites

Ten sites were sampled in each of the Cascade (44°30' - 45°20'N, 122°12' - 122°35'W) and Coast (45°2'- 45°13'N, 123°5' - 123°55'W) Ranges of northwestern Oregon. In the Cascade Range, sites were chosen to represent lichen "hotspots" (as part of a larger study); areas presumed to have high lichen diversity based on forest composition (e.g., Neitlich and McCune 1997). The ten Coast Range sites were chosen to represent areas likely to be targeted for commercial moss harvest. These were stands with some hardwood component to the overstory (red alder, *Alnus rubra* Bong.) and tall shrubs in the understory (e.g., vine maple, *Acer circinatum* Pursh, and *Vaccinium parvifolium* Smith). All stands had vine maple in the understory; a favorite host among commercial moss harvesters in this area. Host species will be described elsewhere (Peck 1997). At each site, approximately 1.5 ha was sampled in July 1994. Characteristics recorded at each site included: percent slope, aspect, dominant vascular plant species, and basal area (BA) of conifers and hardwoods (Table 1). Aspect was adjusted to a 0-180° scale, with north and south at the poles (0 = north; 90 = east and west). Basal area estimates were determined using wedge prism data (BAF = 2.3 m^3/ha = 10 ft^2/acre) at five points. Estimates of elevation and the horizontal and vertical distance to the nearest perennial stream or body of water were taken from topographic maps. Estimates of stand age were taken from timber records (Salem District, BLM; Santiam State Forest; Hebo District, Siuslaw National Forest).

TABLE 1. Ranges in site characteristics for Cascade Range and Coast Range sites, northwestern Oregon. Moss mat mass values are oven-dry weight. Stem density refers to the density of hosts harboring harvestable epiphyte mats.

	Cascade Range Sites	Coast Range Sites
Stand Age (years)	50 - 290	65 - 110
Elevation (m)	75 - 780	120 - 410
Conifer BA (m^2/ha)	12.5 - 40.0	3.0 - 46.5
Hardwood BA (m^2/ha)	1.0 - 21.0	0.0 - 28.5
Stem Density (stems/ha)	340 - 6090	1260 - 7450
Mean Harvestable Moss Mat Mass (g)	19 - 81	23 - 78

Mat Sampling

To approximate the majority of commercial moss harvest in this region, only understory trees and shrubs with commercially harvestable epiphyte mats were sampled. First, "harvestable" mats had to be defined. Based on numerous conversations with commercial moss harvesters between 1991 and 1994, "harvestable" mats were defined as (1) loose mats of nonadherent species (i.e. no appressed or embedded species), which (2) can be harvested from the host in a single, continuous mass, that (3) a commercial harvester in our area would consider "worth removing at this time." The key elements of harvestability appear to be (a) ease of removal, and (b) high volume per mat. Harvestable mats were generally at least 200 cm^3 in volume.

Twenty or twenty-eight tree trunks or shrub stems with harvestable quantities of epiphytes were selected at each site using the point-centered quarter method (Cottam et al. 1953), which was originally developed for sampling tree densities based on tree-to-point distances from systematically located points on a transect. The first point in each transect was at least 50 m from the nearest edge (e.g. road) and points were placed at 50 m intervals. At each point, four quadrants were established. Within each quadrant, the tree trunk or shrub stem with harvestable quantities of epiphytes (hereafter the "stem") nearest the point was chosen for sampling.

Epiphytes were sampled below 2 m in height to approximate current regulations on commercial moss harvest on public lands, which prohibit harvest above 3 m (10'; USDI Bureau of Land Management) or 6.1 m (20'; USFS Siuslaw National Forest), and to reduce measurement error for epiphytes difficult to see from the ground. On each stem, a randomly placed one-meter microplot was stripped of all harvestable epiphytes (the "epiphyte mat"). In the laboratory the epiphytes were sorted by species, their abundance estimated visually as a percentage of the total volume of material from a given stem (after McCune 1990), then oven dried (60°C for 24 hr) and weighed. Nomenclature follows Anderson et al. (1990) for mosses, Stotler and Crandall-Stotler (1977) for hepatics, Esslinger and Egan (1995) for lichens,

and Hitchcock and Cronquist (1973) for vascular plants. Voucher specimens are in the OSU Herbarium, Corvallis, OR.

Calculations

Biomass was estimated for each species by extrapolating from the one meter segment to the entire stem (based on the total length of the stem) and from there to the stand level (based on stem density estimates from the point-centered quarter method; Cottam et al. 1953, Peck and McCune sub.). Gamma, mean alpha, and beta diversity indices were calculated for each of the 20 sites, for all 10 sites in each of the Cascade and Coast Ranges combined, and for all 20 sites combined. Gamma (γ) diversity was measured as the total number of species in all microplots combined. Mean alpha (α) diversity was calculated as the average number of species per microplot across all microplots. Beta (β) diversity, a measure of the amount of community change, was calculated as the ratio of gamma to mean alpha (γ/α).

Pearson correlations were used to evaluate relationships of environmental characteristics to gamma diversity measures. As the primary assumption of ANOVA, independence of samples, was met, ANOVA was used to compare group means between tree trunks and shrub stems for biomass data and for the diversity measures. Because the Cascade and Coast Range sites did not differ significantly for any diversity measure for all cryptogams or for any component group (i.e., mosses, hepatics, or lichens; ANOVA $p < 0.5$), correlations with stand and site characteristics are based on the Cascade and Coast Range data combined.

Indirect Gradient Analysis

To elucidate patterns of abundance among harvestable epiphyte species, I chose to ordinate these data using global nonmetric multidimensional scaling (NMS, McCune and Mefford 1995) with the quantitative version of the Sørensen (1948) similarity index as a distance measure. The data were divided into two matrices (target and nontarget/incidental) based on the frequency and abundance of each species. No outliers were identified in the analyses. Ordinations were interpreted on the basis of Pearson correlations and Kendall's tau (a measure of rank correlation useful for categorical data) between ordination axes and species and stand level characteristics.

Differences in species composition among tree trunks and shrub stems were tested with multiresponse permutation procedures (MRPP, McCune and Mefford 1995; Zimmerman et al. 1985). MRPP is a nonparametric method that tests for multivariate differences among groups (p-values based on a t-statistic). Species indicative of tree trunks or shrub stems were discerned using indicator species analysis (Dufrêne and Legendre in press; program INDICATE, B. McCune unpubl.), which takes both relative abundance and relative frequency into account when assigning indicator values (IV). IV's range from zero (i.e., the species has no value as an indicator of that group) to 100 (i.e., the species perfectly indicate that group). Significance of the IV is evaluated by a Monte Carlo procedure that randomly reassigns sample units to different groups. The resulting p-value is based on the proportion of 1000 random reassignments that result in an IV greater than the observed IV. Species with p-values less than 0.05 and differences in IV values of at least 5 points were considered indicative of the group with the higher IV value.

Results and Discussion

Harvestable Moss Mat Composition

Based on numerous conversations with commercial moss harvesters, I had defined a "harvestable" mat as a loose mat of nonadherent species that could be harvested, with virtually no effort, from the host in a single, continuous mass of at least 200 cm^3 in volume. These mats ranged from 20 to 80 g (oven dry weight; Table 1) and were composed of a variety of mosses, hepatics, lichens, and an occasional vascular plant (Table 2). Clearly, commercial "moss" harvest impacts a larger community than simply epiphytic mosses; a community about which ecological interactions are not well understood. The resistance of this community to disturbance, and thus the sustainability of the community under continued commercial harvest, is equally unknown. For instance, the dispersal capabilities and growth rates of the species in this community may differ substantially, contributing to the return of a very different community than the one that was originally harvested (see Vance and Kirkland 1997).

To aid in the management of sustainability for these communities, the species found in this study

TABLE 2. Epiphytes found in harvestable moss mats, Cascade and Coast Ranges, northwestern Oregon. [4] Denotes ROD Category 4 (ROD 1994) species. I = incidental species, N = nontarget species, T = target species. Data are frequency of occurrence and mean biomass across all microplots for each Range.

	Cascade Range			Coast Range			
Species	% Frequency (n=224)	Biomass kg/ha	SE	% Frequency (n=280)	Biomass kg/ha	SE	Utility
MOSSES							
[4]*Antitrichia curtipendula*	45	13.1	0.6	16	16.9	0.5	T
Claopodium crispifolium	8	4.7	0.2	9	3.9	<0.1	I
Dendroalsia abietina	4	0.3	<0.1	0			N
Dicranum fuscescens	0			1	<0.1	<0.1	N
Dicranum scoparium	<1	<0.1	<0.1	5	17.3	1.0	N
Dicranum tauricum	0			<1	0.1	<0.1	N
Eurhynchium oreganum	14	4.1	0.1	17	10.4	0.2	T
Homalothecium fulgescens	2	0.9	<0.1	0			N
Homalothecium nuttallii	6	1.4	0.1	2	2.6	0.1	I
Hypnum circinale	<1	0.5	<0.1	0			N
Hypnum subimponens	1	0.1	<0.1	<1	<0.1	<0.1	I
Isothecium myosuroides	78	110.0	2.5	97	526.8	10.1	T
Leucolepis acanthoneuron	2	0.8	<0.1	0			N
Metaneckera menziesii	7	16.7	0.6	1	0.1	<0.1	I
Neckera douglasii	79	168.2	4.6	73	238.0	4.8	T
Orthotrichum affine	<1	<0.1	<0.1	0			N
Orthotrichum lyellii	8	0.5	<0.1	20	.6.7	0.3	N
Orthotrichum obtusifolium	<1	0.1	<0.1	0			N
Orthotrichum pulchellum	0			1	<0.1	<0.1	N
Plagiomnium insigne	3	0.1	<0.1	1	<0.1	<0.1	N
Plagiomnium venustum	<1	0.2	<0.1	0			N
Plagiothecium undulatum	0			3	4.1	0.2	N
Rhizomnium glabrescens	0			4	2.3	0.1	N
Rhytidiadelphus loreus	8	8.1	0.4	10	42.1	1.9	T
Ulota crispa	0			3	0.3	<0.1	N
HEPATICS							
Frullania bolanderi	5	0.2	<0.1	2	0.6	0.0	I
Frullania tamarisci subsp. *nisquallensis*	18	8.9	0.4	42	31.8	0.8	T
Lophocolea bidentata	0			<1	<0.1	<0.1	N
Metzgeria conjugata	2	<0.1	<0.1	4	2.0	0.1	N
Porella cordeana	2	<0.1	<0.1	1	0.1	<0.1	I
Porella navicularis	58	19.2	0.3	35	44.7	1.7	T
LICHENS							
Cladonia	1	<0.1	<0.1	7	0.6	<0.1	N
Cladonia ochrochlora	<1	<0.1	<0.1	0			N
Leptogium corniculatum	<1	<0.1	<0.1	0			N
Leptogium polycarpum	1	<0.1	<0.1	0			N
[4]*Lobaria oregana*	1	0.2	<0.1	0			N
[4]*Lobaria pulmonaria*	2	0.2	<0.1	0			N
Menegazzia terebrata	0			<1	<0.1	<0.1	N
[4]*Nephroma laevigatum*	1	<0.1	<0.1	0			N
[4]*Nephroma resupinatum*	0			<1	<0.1	<0.1	N
Parmelia sulcata	4	0.3	<0.1	0			N
[4]*Peltigera collina*	2	0.1	<0.1	1	<0.1	<0.1	N
Peltigera membranacea	0			<1	<0.1	<0.1	N

Continued, next page

Table 2, Continued

Species	Cascade Range % Frequency (n=224)	Cascade Range Biomass kg/ha	Cascade Range Biomass SE	Coast Range % Frequency (n=280)	Coast Range Biomass kg/ha	Coast Range Biomass SE	Utility
[4]*Pseudocyphellaria anomala*	1	<0.1	<0.1	1	0.5	<0.1	N
Ramalina farinacea	2	<0.1	<0.1	0			N
Sphaerophorus globosus	<1	<0.1	<0.1	1	<0.1	<0.1	N
[4]*Sticta limbata*	0			<1	<0.1	<0.1	N
Usnea filipendula group	4	0.2	<0.1	0			N
VASCULAR PLANTS							
Montia sibirica	<1	<0.1	<0.1	<1	<0.1	<0.1	N
Polypodiumglycyrrhiza	<1	<0.1	<0.1	5	2.2	0.1	N

were separated into three qualitative and quantitative categories on the basis of (1) *a priori* knowledge of the species found in commercially sold moss, and (2) the relative frequency and abundance of species found in this study. Seven species were defined as "target" species based on their predominance in commercially sold "moss" (unpubl. data) and their high frequency and abundance in the current study(>10% frequency and > 10 kg/ha of harvestable biomass); *Antitrichia curtipendula*, *Eurhynchium oreganum*, *Frullania tamarisci* subsp. *nisquallensis*, *Isothecium myosuroides*, *Neckera douglasii*, *Porella navicularis*, and *Rhytidiadelphus loreus*. Together, these species composed more than 90% of the total biomass of harvestable epiphytes in these sites.

Among the remaining 43 species, two categories of species were quantitatively discerned. Six species, considered "incidental" species (Table 2), are not generally targeted for commercial harvest because of their low frequency of occurrence but are nonetheless not discriminated against by commercial harvesters (pers. obs.). These incidental species typically had a frequency of >5 but < 10% and had >5 but < 10 kg/ha of harvestable biomass, except for *Metaneckera menziesii*. While locally abundant, *M. menziesii,* which typically occurs on big leaf maple, *Acer macrophyllum* Pursh, is generally unacceptable for harvest because older portions of the plant turn bright yellow-orange. True "nontarget" species (Table 2) consisted of most hepatics, and all lichens and vascular plants. These 37 species are not generally acceptable for harvest due to poor color or texture. Nontarget species typically occurred in < 5% of samples and had an estimated biomass of < 5 kg/ha. The nontarget species *Dicranum scoparium* and *Orthotrichum lyellii* were exceptions. Although common, these species exhibit growth forms (individual tufts) generally undesirable for moss harvest. Collection of nontarget species by commercial harvesters should, at this time, be considered accidental. While some harvest of lichens does occur, none of the species found in this study occurred in large enough abundance to be targeted for harvest in this area.

It is important to note that the assignment of categories such as "target," "incidental," and "nontarget" derives from its usefulness to managers. Harvesters rarely recognize differences among individual species of bryophytes, with the exception of *Rhytidiadelphus loreus* (called "big red stem" by harvesters). Rather, they seek large quantities of abundant mosses of the right color and texture and thus, functionally, target moss mats to a greater extent than individual species. However, these moss mats are often composed of a consistent flora—the target species.

Although no rare, threatened, or endangered species were found, one target and seven nontarget species are listed as Category 4 (ROD 1994) species, requiring general regional surveys (Table 2). Their presence in these stands, and stands included in other epiphyte studies (A. Rosso pers. comm. 1996), suggests that some of these species may be more common than previously believed. However, given that the rate and the impacts of commercial moss harvest are unknown, permitting harvest of species that may become classified for active management is somewhat of a gamble.

Harvestable Moss Mat Diversity

In both mountain ranges, a typical harvestable mat had three to four species, most of which were

target mosses or hepatics (mean alpha diversity, Table 3). Harvest in a typical stand would reduce the populations of 6-7 target species, 2-3 incidental species, and 5-6 nontarget species, and an occasional ROD (ROD 1994) listed Category 4 lichen. Total cryptogamic gamma diversity across mountain ranges was 48; mean alpha diversity was 3.6 and beta diversity was 13.3. The large range in gamma diversity among sites, and subsequently the high beta diversity, is primarily a function of variability in the presence of nontarget species in these mats. Although the same target species occurred in most mats, nontarget species differed from site to site and even from mat to mat within sites. This is because (a) harvesters consistently seek out target species and generally ignore nontarget and incidental species, and (b) nontarget and incidental species tend to be either rare on the landscape in general or most common on other substrates, such as the forest floor (*Leucolepis acanthoneuron*, *Plagiomnium venustum*), logs (*Hypnum circinale*, *Plagiothecium undulatum*, *Rhizomnium glabrescens*), or the canopy (*Pseudocyphellaria anomala*, *Sticta limbata*), and occur only occasionally as understory epiphytes.

Lichen gamma diversity showed no pattern in relation to any stand characteristics. Moss gamma diversity increased when a higher proportion of sampled stems were tree trunks ($r = 0.49$), particularly red alder (*Alnus rubra*; $r = 0.59$), but decreased when conifer basal area was higher ($r = -0.72$). Gamma diversity for hepatics increased only when host surface area was higher (i.e., larger trees; $r = 0.49$). These results indicate that the harvestable epiphyte communities on hardwood tree trunks are distinct from those on shrub stems. Host surface area, epiphyte mat mass, and overall species richness were all substantially higher on tree trunks than shrub stems (ANOVA, $p < 0.001$) and species composition was significantly different between tree trunks and shrub stems for both mountain ranges (MRPP, $p < 0.001$). While only the target species *Isothecium myosuroides* strongly indicated shrub stems, several nontarget and incidental species indicated tree trunks (Table 4).

TABLE 3. Totals (ranges among sites in parentheses) in cryptogamic diversity of epiphytes found in harvestable moss mats in the Cascade and Coast Ranges, northwestern Oregon. Alpha diversity, α, is the average number of species per mat. Gamma diversity, γ, is the total number of species accumulated from all mats per site and per range. Beta diversity, β, is a measure of community change, calculated is γ/α. ROD = Category 4 (ROD 1994) survey and manage species.

	Cascade Range Sites	Coast Range Sites
α	3.5 (2.5-4.0)	3.7 (1.5-5.8)
γ	37 (8-18)	32 (6-21)
β	10.6 (2.9-5.3)	8.6 (2.9-4.6)
Species Richness		
Mosses	19 (5-13)	18 (3-12)
Hepatics	5 (2-5)	6 (2-4)
Lichens	13 (0-9)	8 (0-3)
No. Target Species	7 (5-7)	7 (5-7)
No. Incidental Species	6 (1-4)	6 (0-4)
No. Nontarget Species	26 (1-11)	21 (1-14)
No. ROD listed lichens	5 (0-5)	4 (0-2)

Although epiphytic bryophyte diversity has been studied in the Pacific Northwest by a number of researchers (Coleman et al. 1956; Hoffman and Kazmierski 1969; Hoffman 1971; Kenkel and Bradfield 1981, 1986; Peck et al. 1995; A. Rosso pers. comm. 1996), direct diversity comparisons between these studies and the current study are

TABLE 4. Indicator values for epiphytes found in harvestable moss mats on shrub stems and tree trunks, northwestern Oregon. IV = indicator values. Species with large IV's for a group are strong indicators for that group. Only species with p values < 0.05 and diffferences in IV's of 5 points are listed.

	IV			IV	
Species	Shrubs	Trees	Species	Shrubs	Trees
Claopodium crispifolium	1	20	*Metzgeria conjugata*	0	9
Dicranum scoparium	0	10	*Plagiothecium undulatum*	0	9
Eurhynchium oreganum	3	25	*Polypodium glycyrrhiza*	0	8
Isothecium myosuroides	58	26	*Porella navicularis*	17	37
Leucolepis acanthoneuron	0	6	*Rhytidiadelphus loreus*	2	14
Metaneckera menziesii	0	20			

not possible as these studies involved collections of all epiphytes present, whereas the current study only included species found in harvestable epiphyte mats. By definition, therefore, the current study does not include many appressed species (e.g. *Radula*). However, diversity values in the current study were not outside the range of those found in these studies.

The species list overlaps considerably with other epiphyte studies in the Pacific Northwest. Nineteen out of 29 epiphytes found on *Acer macrophyllum* over five sites in British Columbia (Kenkel and Bradfield 1986) were also found in the current study. In a study of conifers in British Columbia, Peck et al. (1995) found 33 species of epiphytes, 10 of which were also found in the current study. Of 44 bryophytes found in an extensive study of epiphytes on shrubs in the Oregon Coast Range (A. Rosso pers. comm. 1996), 24 were also found in harvestable epiphyte mats. Although the relative overlap among these studies may appear low, these studies included a broader range of bryophytes than only those occurring in harvestable quantities. In that light, the degree of overlap indicates that harvestable epiphyte mats are composed of several species, particularly target species, that are common and abundant throughout the Pacific Northwest.

Variation in Harvestable Moss Mat Communities

Ordinations were performed on two subsets of the combined Cascade and Coast Range data matrix; the "target species" dataset (seven species) and the "nontarget and incidental species" dataset (18 species), which included only species with an frequency of occurrence of >5% in at least one mountain range. Both ordinations were rotated such the basal area of conifers was aligned with axis one to facilitate interpretation.

Ordination of the target species dataset produced a two dimensional solution accounting for 82% of the variability in the data (Figure 1a). The first axis, which explained 57% of the variation, was positively correlated with all target species ($r > 0.5$) except *Antitrichia curtipendula* ($r = 0.1$), and contrasted stands with high hardwood basal area ($r = 0.51$) and stands with high conifer basal area ($r = -0.67$). Target species, except *Antitrichia*, were most abundant in stands with high hardwood basal area. The second axis, which explained 25%

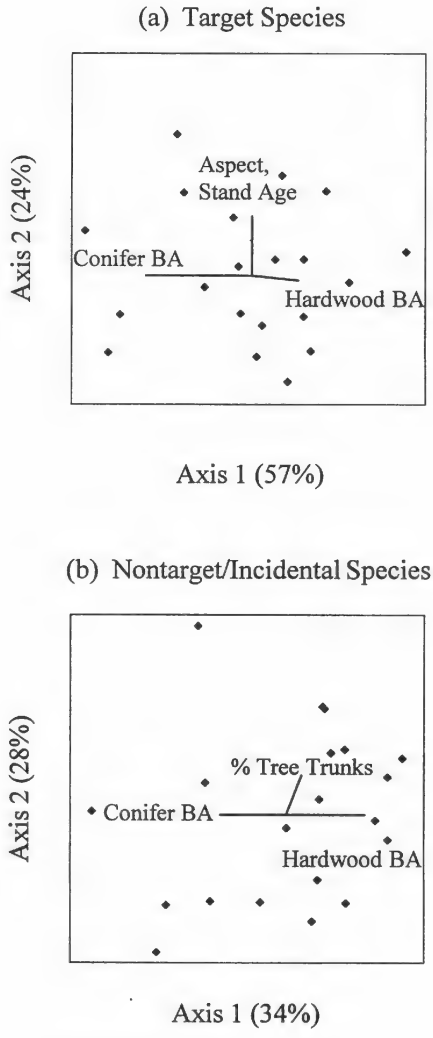

Figure 1. NMS ordinations based on target species (a; seven most common and abundant species), and nontarget/incidental species (b; 18 less common and abundant species), Cascade and Coast Ranges, northwestern Oregon. Diamonds are sites. Line lengths represent the strength and direction of correlations of site characteristics with axes. Both ordinations indicate that epiphytes found in harvestable moss mats are least abundant in stands with high conifer basal area and most abundant in stands with high hardwood basal area. The target species *Antitrichia curtipendula* was less abundant in older, drier stands, while the greater abundance of several nontarget/incidental species on tree trunk hosts transcended other environmental factors.

of the variability in the data, was strongly correlated with *Antitrichia curtipendula* (r = -0.76), and contrasted older (stand age r = 0.47), drier (aspect r = 0.57) stands with younger, wetter stands. *Antitrichia curtipendula* was less abundant in the older, drier stands, despite being typically considered an old-growth associate (ROD 1994). Its presence in these younger stands suggests that its association with old-growth may be a function of general environmental conditions not necessarily specific to old-growth.

The nontarget/incidental species dataset had a two dimensional solution accounting for 62% of the variability in the dataset (Figure 1b). The first axis explained 34% of the variability and was positively correlated with the abundance of the mosses *Claopodium crispifolium* (r = 0.62), *Dicranum scoparium* (r = 0.43), *Homalothecium nuttalli* (r = 0.43), *Orthotrichum lyellii* (r = 0.49), *Plagiothecium undulatum* (r = 0.41) and *Rhizomnium glabrescens* (r = 0.43) and the vascular plant *Polypodium glycyrrhiza* (r = 0.45), and negatively correlated with the lichen *Lobaria pulmonaria* (r = -0.53). This axis also contrasted stands with high hardwood basal area (r = 0.59) and those with high conifer basal area (r = -0.61). These nontarget and incidental species were most abundant in stands with high hardwood basal area, except the canopy lichen *Lobaria,* which was most abundant in stands with high conifer basal area. Greater harvestable epiphyte abundance in areas with high hardwood basal area (and lower abundance in conifer dominated sites) supports previous indications that hardwoods are important for epiphyte communities (Neitlich and McCune 1997, Rambo and Muir 1995). The second axis, which explained 28% of the variability, was positively correlated with the proportion of tree trunks sampled r = 0.44). This axis was positively correlated with *Claopodium crispifolium* (r = 0.52) and *Metaneckera menziesii* (r = 0.45), both predominantly tree trunk epiphytes. Again, nontarget/incidental species appear to be associated with hardwood tree trunks to a greater extent than understory shrubs.

Cascade Range and Coast Range sites did not separate in the ordinations when analyzed together and separate analyses of the target species for each range revealed essentially identical patterns. The primary difference between ranges was the complexity of the gradients influencing harvestable epiphyte abundance, with epiphyte abundance in the Cascade Range related to aspect, slope, hardwood basal area, and the linear distance to water, which were not important in the Coast Range. This complexity, however, may simply reflect the wider geographic range, and larger spread of stand ages (from 50 to 290) of the Cascade Range sites relative to the Coast Range sites. In addition, the Cascade Range sites were chosen as areas of high lichen diversity. Although average moss and hepatic species richness did not differ between the two ranges, it is impossible to quantify what effect this difference in site selection had on the comparison of the two mountain ranges. Of all 50 species, twenty-three species were common to both mountain ranges (Table 2), including all target and incidental species. In the Cascade Range, *Isothecium myosuroides* contributed 31%, and *Neckera douglasii* 47%, to total harvestable biomass. Their roles were reversed in the Coast Range, where *I. myosuroides* and *N. douglasii* contributed 55% and 25% of the harvestable biomass, respectively.

Management Implications

It is important to note that the definition of what is considered harvestable by commercial moss harvesters will depend on demand; as restrictions on moss harvest increase on some public lands, moss mats previously considered marginal will begin to be harvested simply because they are still available on other private and public lands. A shift in this direction would likely lead to increased harvest of incidental species, and of the nontarget species associated with those communities. One of the most important findings of this study is the discovery that commercial moss harvest impacts a significantly larger community than the handful of most abundant mosses, including ROD (1994) listed lichens. The inadvertent harvest of species that may someday require active management suggests that restrictions discouraging the harvest of these species may be appropriate.

Identifying and quantitatively distinguishing categories of target, incidental, and nontarget species will enable managers to direct harvest away from areas with more sensitive species. Managers should protect some areas from harvest (e.g., Late Successional Reserves to be managed toward "old growth" conditions) to facilitate the continuity that may be required to develop complex, mature epiphyte mats. The actual impact

of moss harvest on nontarget and incidental species can only be evaluated by examining the abundance of these species on other substrates, particularly in cases where these species occur primarily as non-epiphytes. The general surveys required for many lichen and bryophyte species listed in the ROD (1994) should provide an opportunity to survey for other species that are impacted by commercial moss harvest. The broad geographic distribution of common epiphytic bryophyte species suggests that some level of commercial moss harvest may be acceptable over the landscape if pockets of target species can be identified for harvest, or conversely, if pockets of nontarget/incidental species can be identified for protection.

There are several obstacles to determining what level of commercial moss harvest is acceptable on the landscape. First, basic inventory information is lacking about the landscape level distribution and abundance of harvestable mosses. Case studies such as the current study aid local mangers, but ultimately widescale inventories will be required in order to determine the magnitude of the resource base and to evaluate patterns of abundance in relation to stand characteristics such as the presence of a hardwood component in the overstory. Second, the ecological roles of harvestable mosses are virtually unknown. Landscape level inventories should incorporate sampling designed to evaluate the role of harvestable mosses as food and habitat for invertebrates, as regulators of nutrient and water cycling in the forest ecosystem, and as sources of diversity in the epiphytic and cryptogamic communities.

The most pressing need, however, is for public land managers to come to a consensus on which aspects of "sustainability" need to be managed. Harvestable epiphytes are a multifaceted resource. In addition to their ecological roles, they provide income for local residents with a long tradition of supplemental income derived from public lands and they provide a level of aesthetics to which residents of the Pacific Northwest are accustomed. Sustainability must be defined, whether it be as sustainability of harvest volumes, of continuity for old-growth moss mat development, or of a rich mantle of green adorning our forests.

Summary

In twenty sites in northwestern Oregon, harvestable moss mats ranged from 20 to 80 g (dry weight) and were composed of 50 species of mosses, hepatics, lichens, and an occasional vascular plant. The most common and abundant species, which are targeted for commercial harvest, are most abundant in stands with high hardwood basal area. These species are common and abundant throughout the Pacific Northwest. Less common and abundant species, which are often incidentally harvested, are also more abundant on large surface-area hosts (i.e., mature hardwoods). These nontarget and incidental species contribute a large proportion of the diversity of the harvestable epiphyte community and can be protected if harvest is directed away from mature hardwood dominated forests.

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Allocation, Growth and Estimated Population Structure of *Corydalis aquae-gelidae*, a Rare Riparian Plant

Abstract

The pattern of biomass allocation to roots, shoots and reproductive parts, the growth rate, and the population structure, in terms of both stages of development and age, were determined for *Corydalis aquae-gelidae*. The species had a relatively high allocation to belowground structures (adult belowground/aboveground ratio of about 2), largely in the form of starch storage tissue. The allocation to reproduction was relatively low (8%). The growth rate was slow, with an estimated 7 years (6-9 years, with 95% confidence) required for reproductive maturity. This herbaceous perennial appeared to be a stress-tolerator, whose populations would not rebound quickly after disturbance. The population age structure, estimated from a growth model and size measurement of 25 plants in successive years, implied successful reproduction. The methods developed here provided management-related information, including estimates of growth rates, population structure and current reproductive success, as well as probable response to disturbance and the species' successional status. These methods required only two years of data, and could be used for other herbaceous perennials.

Introduction

Conservation of rare plants requires understanding of their biology and population status: are they reproducing effectively, and how might they respond to disturbance or manipulations intended to aid their persistence? Population status can be determined using long-term studies that monitor population changes (Owen and Rosentreter 1992, Law 1983), following changes in plant numbers, or the survival and reproduction of individuals. Alternatively, population status can be estimated from current population age structure (Crisp and Lange 1976); for example, age structures can be used to help ascertain if adequate reproduction has been occurring. For many herbaceous species, however, estimating the age of individuals is tedious or impossible. Estimates of the age of individuals can be made, however, if plant sizes are known and if growth rates for a given plant size can be measured.

The concept of plant adaptive strategy allows one to use combinations of characteristics of a species to predict how it will respond to environmental change or disturbance. Hypotheses about plant strategy include those of r,K selection (MacArthur and Wilson 1967, Pianka 1970), and the competitive, stress-tolerant, and ruderal strategies of Grime (1979). Plant species with different strategies vary in their rates of growth, and in their allocation of resources to different functions, e.g., to reproduction or storage. For example, stress-tolerators are slow growing plants of relatively unproductive environments, which allocate relatively more resources to storage and long-term survival.

We used measurements of allocation, plant size, and growth rate to estimate the strategy and population status of a rare plant, *Corydalis aquae-gelidae* Peck & Wilson, Fumariaceae (cold-water corydalis), that cannot be aged directly and for which there is little biological information. Information about this species' growth rates and allocation patterns indicated a stress-tolerant plant that may not respond well to disturbance, while the estimated population age structure indicated a stable, successful population.

Study Area

This study was conducted in the southwest portion of the Mount Hood National Forest, Oregon (45° N latitude and 122° W longitude), with sampling at Rhododendron Creek and nearby on the upper Clackamas River. Vegetation is representative of the *Tsuga heterophylla* zone of Franklin and Dyrness (1973), with streamside forests dominated by *Tsuga*, *Thuja plicata* and *Alnus rubra*. Growth measurements were recorded for plants in a 7x2 m plot on a gravel bar between the main stem and a side channel of Rhododendron Creek.

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The plot was in typical conditions for *Corydalis aquae-gelidae* (Goldenberg 1992): moist, coarse mineral substrates in or next to the stream, with few herbaceous competitors and fairly dense tree canopy cover.

Study Species

Corydalis aquae-gelidae is locally endemic in northwestern Oregon and southwestern Washington. It is an herbaceous perennial without vegetative reproduction. The shoots arise from large, fleshy taproots and grow to over one meter tall. The species grows in or within 2 m of flowing water, along spring-fed streams with relatively little variation in flow rate (Goldenberg 1992). It is a US Fish and Wildlife Service species of concern, and a candidate for listing under the Oregon Endangered Species Act (Oregon Natural Heritage Program 1995). Its habitat has been disturbed by logging, fish habitat improvement, and hydropower development. Information useful for evaluating its population persistence and reaction to streamflow reduction and streambank manipulation is needed to aid in its conservation.

Methods

On September 5, 1990, near the end of the growing season, 25 plants were marked by placing a numbered tag at a recorded distance and direction from their base. The plants were classified into four growth stages: reproductive adults, non-reproductive adults (smaller plants with a stem but no flowers), juveniles (very small, stemless plants), and seedlings (first-year plants with cotyledons but usually no true leaves). The sample included five reproductive adults, one non-reproductive adult, nine juveniles, and ten seedlings. The number of leaves, the total length of the leaf blades, plant height, and the number of fruiting pedicels were recorded for each plant. All fruits were dehisced (only pedicels remained), but the plants had not begun senescence.

On September 10, 1991, these plants were remeasured. The shoots were harvested and separated into stems, leaves (including petioles), and raceme axes (pedicels and peduncles), and oven-dried. In addition, three reproductive adults (two including roots), six juveniles with roots and five seedlings with roots were collected from a nearby side channel of the Clackamas River, separated into parts, and oven-dried. Fine roots were collected to the extent possible.

During July, 1991, thirty flowers were collected from five plants outside the study plot at Rhododendron Creek. The flowers were dried and weighed after the pistils were removed. Nine fruits and twenty-five seeds were also collected during August. The number of seeds per fruit was recorded for 122 fruits at Rhododendron Creek and the Clackamas River.

Dry mass of reproductive structures was used to estimate the dry mass lost from each pedicel on the plants collected in September, 1991. For each reproductive adult, total flower mass was estimated as the number of pedicels multiplied by mean sampled flower mass, and likewise for total fruit and total seed mass. Leaves produced early in the season do not senesce in mid-season, but rather at the end of the season along with the entire plant, therefore sampling in September only had to account for reproductive structures lost at an earlier date. An allometric regression of root mass on total estimated shoot mass was used to estimate root mass for plants whose roots were not sampled.

Statistical Analyses

A series of regressions was made relating the proportional mass of each plant part to the total estimated mass, using Statgraphics (STSC 1991). These regressions provided a model of how biomass allocation varies with total mass. Scatter diagrams and residual analyses were used to determine appropriate transformations and the order of the regression equations.

A linear relationship between root mass and shoot mass was calculated (equation 4, table 1). The allometric constant is the slope of this regression line (Hunt 1990). The root mass estimated from equation 4 for the largest reproductive adult whose roots were sampled was far from the observed value (20.53 g, vs. 15.91 g observed); therefore, a quadratic model was fitted (equation 5, table 1). Equation 5 gave a much more realistic estimate (e.g. 16.36 vs. 15.91 g observed) for the reproductive plants, had a higher adjusted r^2, and was used to estimate root masses where roots were not sampled. The linear model is presented, however, as this is often used as the standard relationship (Hunt 1990).

For those regressions that showed no statistically significant relation between total biomass and allocation to a particular plant part ($P>0.05$),

TABLE 1. Regression models relating root and shoot mass. All masses are in grams.

4. ln (root mass) = 1.00 + 0.972 ln (shoot mass)
   n=12 P<0.0001 r^2=0.993 adjusted r^2=.993
5. ln (root mass) = 1.09 + 0.868 ln (shoot mass) - 0.0226 (ln (shoot mass))^2
   n=12 P<0.0001 r^2=0.996 adjusted r^2=.995

the methods in Neter et al. (1989) and the suggestions of Peterman (1990) were used to determine the detectable effect size (DES) in the slope of the regression equation. The DES is a function of the chosen alpha (the significance level), beta (statistical power) and the degrees of freedom. The DES was calculated using a desired alpha of P=0.05 and power of 95%, and six degrees of freedom. The DES represents the smallest population mean slope that could be detected (found to be statistically significant), given the sample size and analysis method.

Relationships Between Age, Stage and Size

To estimate the size at first reproduction, 130 adult plants from 111 population survey plots from throughout the southwestern Mt. Hood National Forest (from Goldenberg 1992) were used to calculate the proportion of plants flowering at different sizes, measured by the number of leaves. Leaf number was converted to mass using an allometric equation derived from the destructive samples. An equation was determined relating leaf mass to proportion flowering. This equation was used to estimate the weight of plants where 10%, 50% and 90% of plants were flowering. Plant age was estimated from plant mass, using the growth model, as the year at which plants were predicted to first equal or exceed the given mass.

Growth Model

To construct a growth model, the total mass of each plant in the sample plot was estimated using the plant's total leaf blade lengths for both year one and year two and regression equations 13 and 5 (see results), except where actual shoot masses were sampled.

Mean relative growth rate (*RGR*) was calculated for each of the 25 sample plants using the equation (Hunt 1990, p. 26):

$$RGR = (\ln M_2 - \ln M_1)/(t_2 - t_1). \quad (1)$$

where M_i is dry mass at the time t_i. This equation was used to give a mean growth rate for the year. To determine *RGR* as a function of plant mass, *RGR* was regressed against the natural logarithm of year one mass to yield the regression equation:

$$RGR_{Mt} = a + b \ln M_t \quad (2)$$

We used the iterative exponential growth model:

$$M_{t+1} = M_t \exp (RGR_{Mt}) \quad (3)$$

where $RGR_{Mt} = a + b \ln M_t$. The observed mean seedling mass was used for M_1. If *RGR* decreases with increasing plant mass, the model yields a sigmoidal curve; growth is exponential, but as *Mt* approaches exp (*-a/b*), RGR_{Mt} approaches 0, and M_{t+1} approaches M_t. Equation 3 may be derived from equation 1, with t_2-t_1=1. Equation 3 is also similar to the general model for exponential growth (Hunt 1990, p. 84), $M = M_o \exp (r\,t)$, with r=*RGR* and t=1.

Population Age Structure

The population structure of 2615 plants in the population survey plots (Goldenberg 1992) was calculated as the percentage of plants in each of the four growth stages: reproductive adults, nonreproductive adults, juveniles, and seedlings. A hypothetical age structure was generated with these percentages, and the age range for each stage estimated from the growth model. An exponential decay function was fitted algebraically to the resulting histogram.

Results

Allocation

The regression equations in table 2 were used to build a model of *Corydalis aquae-gelidae* allocation patterns. The regressions for the reproductive parts were not significant (table 2, equations 9-12), which implies the possibility of constant reproductive allocation. Because the regression slope detectable effect sizes (DES) were large for equations 9-12, a conclusion of no biologically significant change in reproductive allocation with increasing total mass was not war-

TABLE 2. Regression models describing allocation to plant structures as a function of total mass. Equations 7 to 12 applied only to adults. "Racemes" included only peduncles and pedicels, the supporting structures. All masses are in grams.

6. root mass/total mass = 0.777 - 0.0175 ln (total mass) - 0.00504 (ln (total mass))^2
   n=37 P<0.0001 r^2=0.91
7. stem mass/total mass = 0.125 - 0.0642 ln (total mass) + 0.0130 (ln (total mass))^2
   n=8 P=0.0002 r^2=0.97
8. leaf mass/total mass = 0.0708 + 0.0378 ln (total mass)
   n=8 P=0.0038 r^2=0.78
9. raceme mass/total mass = -0.000681 + 0.0021 ln (total mass)
   n=8 P=0.14 r^2=0.32
10. flower mass/total mass = 0.0176 - 0.000697 ln (total mass)
    n=8 P=0.66 r^2=0.04
11. fruit mass/total mass = 0.0215 - 0.000854 ln (total mass)
    n=8 P=0.66 r^2=0.04
12. seeds mass/total mass = 0.0510 - 0.00203 ln (total mass)
    n=8 P=0.66 r^2=0.04

ranted, however. Therefore, the equations are presented as hypotheses which require more data for evaluation. All of the regression equations were used in the allocation model (table 3), so that the total allocation proportions always added to about one, regardless of total mass. The largest plant sampled completely had 23.9 g total mass.

Allocation to roots was large but declined as plants increased in size (table 3). Allocation to roots peaked in juveniles at 0.2 grams total dry mass, which was about the third growing season, according to the growth model. The thickened roots functioned as storage tissue; they had a starch grain concentration comparable to that of potatoes. Fibrous root mass was small compared to that of the thickened storage roots. As total plant mass increased, the mass of the leaves and stems increased at the expense of roots; stems increased at a greater rate than leaves. Larger plants apparently required relatively more supporting structure.

TABLE 3. Proportional allocation of dry matter estimated for *Corydalis aquae-gelidae* of varying total masses. Calculated using equations 6 through 12. Growth stages include seedlings (0.009 g), juveniles (0.2 g) and two sizes of reproductive adults (10 and 25 g).

Total mass (g)	0.009	0.2	10	25
Roots	0.73	0.79	0.71	0.67
Shoots	0.27	0.21	0.29	0.33
Root/Shoot ratio	2.70	3.76	2.45	2.03
Stems			0.046	0.053
Leaves			0.158	0.192
Raceme axes			0.007	0.006
Flowers			0.016	0.015
Fruits			0.020	0.019
Seeds			0.046	0.044
Reproductive total			0.089	0.084

Growth Model

Relative growth rate (RGR) peaked in juveniles, rather than seedlings, and then declined as plant mass increased (figure 1). Outliers with low or negative RGR were removed, due to their poor growth; the intention of this model was to illustrate the growth of healthy plants in favorable microsites. The iterative model given in the methods (equation 3) yielded a time course of dry mass gain (figure 2). Values for the confidence limits for the slope and intercept terms in the regression (figure 1), as well as the mean values, were used in the model to show the possible variation in the growth rates. The mean regression model did not reach an asymptote with any realistic size; this reflects the fact that some of the largest plants sampled grew substantially. Larger plants must be sampled in order to estimate a maximum size for the species.

Figure 3 shows the relationship between the actual and predicted masses for the plants in year two. Because the actual year two masses were used to determine the model parameters, this plot can not be used as model validation. The plot does support the validity of the general form of the growth model, however.

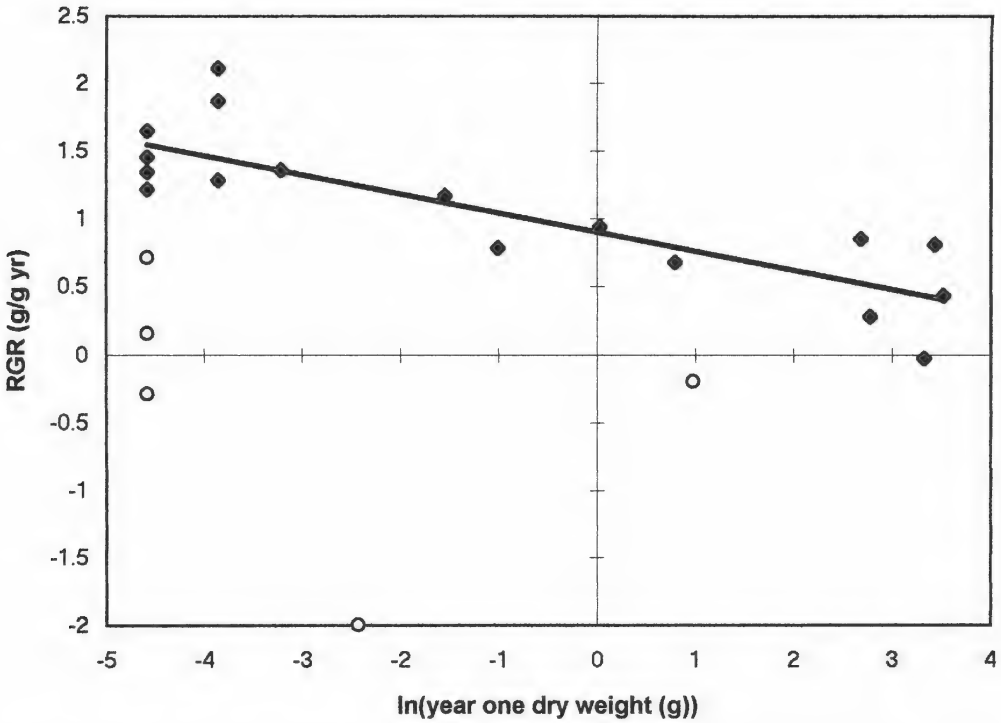

Figure 1. Relationship of the relative growth rate (RGR) to the total dry plant mass in the first sampling year. The outliers specified by circles were removed from the regression due to their poor growth. RGR = 0.9011 - 0.1408 ln(year one mass, g), n=18, r^2=0.71, P=0.0001. The 95% confidence interval for the intercept and slope were 0.7374 to 1.065 and -0.1882 to -0.0934 respectively. Some points represent greater than one sample. First year seedlings are represented by the first column of data points.

Relationships Between Age, Stage and Size

The mass of plants at growth stage transitions was estimated. Seedlings are, by definition, only first year plants. The size of seedlings at the end of their first growing season averaged 0.009 g (n=5, range 0.0045 to 0.0150). One plant in the plot changed from juvenile to non-reproductive adult between the sampled years, with estimated total mass in year two being 2.64 grams, which was used as the size of first stem production.

Total mass at which 10%, 50% and 90% of the plants were flowering was calculated as 4.2, 4.8 and 6.4 grams, respectively, using equation 15 (table 4). The non-linear regression in equation 15 was run using data points for leaf numbers of 4 to 14 with leaf number being converted to mass using equation 14. No plants were flowering at 4 leaves, while all plants were flowering at 10 leaves and above. Estimates for ages of different sized plants were calculated (table 5). Using the growth model, it is estimated that the first stem would develop in the sixth year, and reproduction would begin about the seventh year.

Population Age Structure

Population survey plots (n=111) contained 2615 *Corydalis aquae-gelidae* plants, with 38% seed-

TABLE 4. Regression models used in the growth analysis. All masses are in grams.

13. ln (shoot mass) = -6.30 + 1.47 ln (total blade lengths, cm)
n=21 P<0.0001 r^2=0.98
14. ln (total mass) = -0.287 + 1.23 ln (leaf no.)
n=11 P<0.0001 r^2=0.94
15. proportion flowering = 1 - 64.56 exp (-1.014 total mass)
n=11 P<0.0001 r^2=0.93

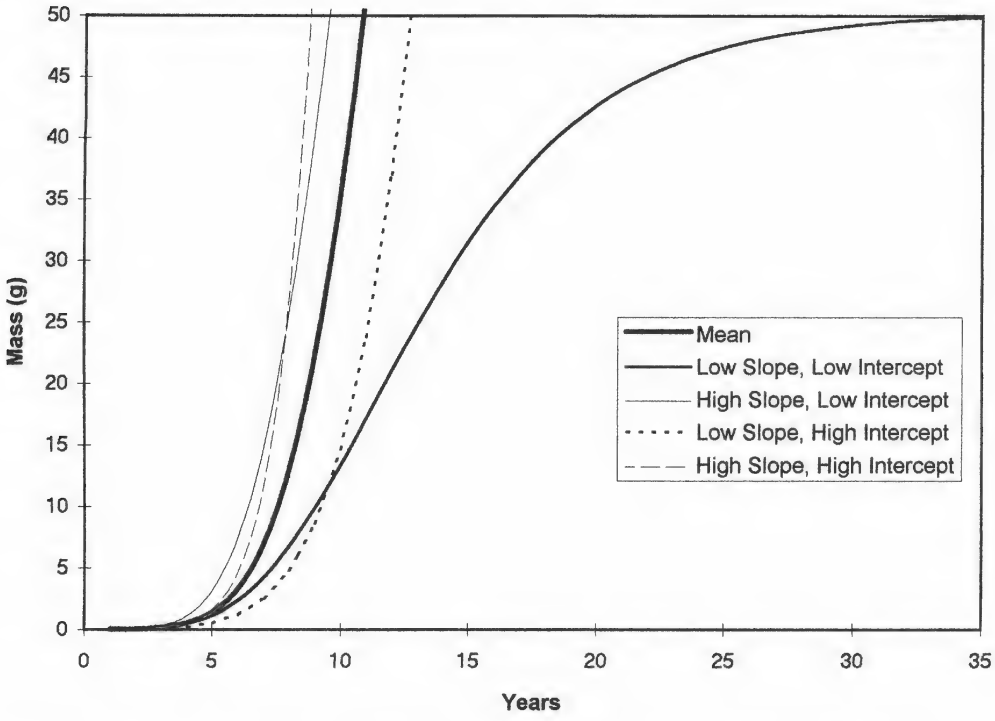

Figure 2. Increase in total plant dry mass with age, as calculated from a growth model. Reproduction began between 4 and 7 grams. The largest plant used to develop the growth model was 70 g; the largest plant weighed (root mass estimated) was 217 g. The 5 lines represent models using the mean regression coefficients and 95% confidence interval coefficients for the slope and intercept, as parameters for the relative growth rate regression equation (equation 3).

TABLE 5. Estimated ages in years at which plants reach specified masses. Estimates were calculated using the mean regression values and 95% confidence interval limits for the slope and intercept in the iterative growth model. The combination of slope and intercept confidence limits giving the widest confidence interval are displayed.

		Years		
Growth stage	Mass (g)	Mean	Lowest estimate	Highest estimate
First stem	3.15	6	5	8
10% reproductive	4.2	7	6	8
50% reproductive	4.8	7	6	9
90% reproductive	6.4	7	6	9
Largest plant in the plot	70	12	10	a
Largest weighed plant[b]	217	17	12	a

a = asymptotic near 50 grams for the slowest-growing model.
b = root mass estimated using equation 5.

lings, 49% juveniles, 3% non-reproductive adults and 10% reproductive adults. There were no significant differences in these percentages among four geographic subareas (Goldenberg 1992). The duration of each stage was estimated from the growth model, with a hypothesized maximum age of 25 years (this maximum age is entirely hypothetical, but appears reasonable, as the age of the largest plant was estimated at 17 years (table 5)). The durations include one year for seedlings, four years for juveniles, one year for non-reproductive adults, and 19 years for adults. A density histogram depicting the age structure was formed by dividing the percentages given above by the duration in each stage, and an exponential curve was fitted to the histogram to approximate a survivorship curve (figure 4). The age structure, with its large number of seedlings, suggests successful reproduction and population maintenance. Fecundity and mortality appeared to be consistent, because of the

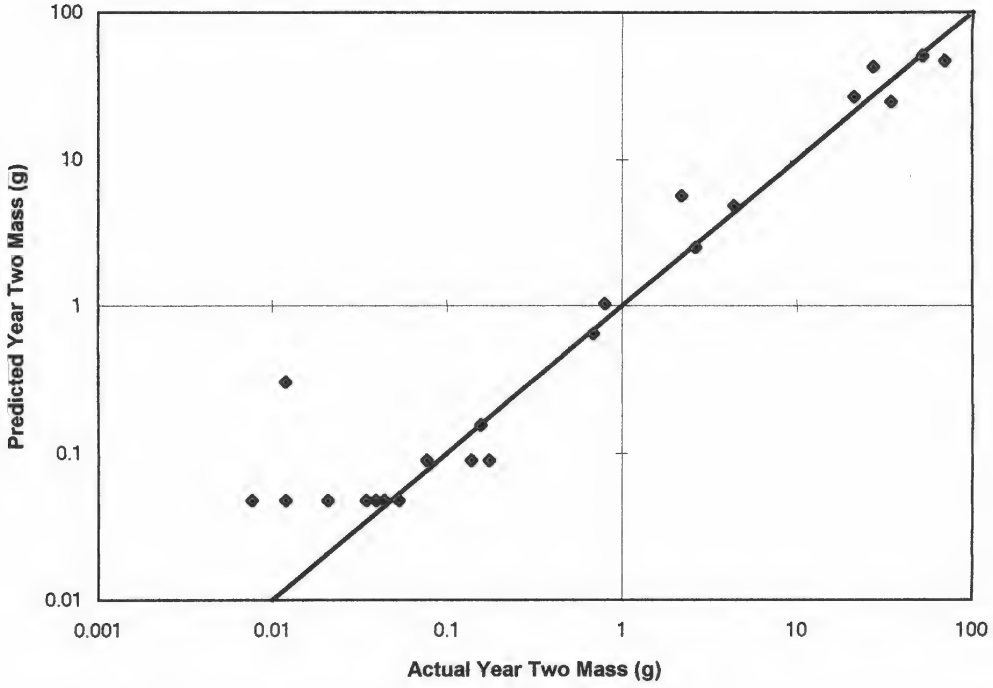

Figure 3. Relationship between actual year two masses and predicted year two masses based on year one masses and the growth model equations. A logarithmic scale was used to show the patterns at smaller sizes. The line represents equality of actual and predicted values.

descending curve of the age structure (the data fits an exponential decay curve), and because of the lack of differences among the geographic areas.

Discussion

Growth and Age Structure Methods

Information valuable for rare plant management, rates of growth and development and a population age structure, was obtained with only two seasons of data collection. In contrast, other methods of obtaining this information, e.g., by constructing life tables, would require the collection of many years of data on a much larger number of plants. The methods developed here should be useful to resource managers with a limited budget, who need relatively quick results.

The extrapolation of the data presented here to *Corydalis aquae-gelidae* throughout its range must be viewed as tentative. Additional sampling would be necessary to give results that could be validly applicable to the plant throughout its range. A larger sample size, with randomly selected samples taken from throughout the area of interest, would be necessary to capture possible regional variation in growth and allocation patterns. With a rare plant, destructive sampling must of course be minimized, and calculating relative growth rate as a function of plant size (e.g., total length of leaves) rather than weight, removes the necessity to harvest the plants. Retaining data from some plant populations for independent model validation would additionally help to test the broad applicability of the results.

An estimation of population age structure which uses these methods requires certain plant behaviors. Consistent fecundity and mortality may be a requirement. If good seedling production only occurs in certain years, for example, interpretation of a single year's data may be difficult. This problem can be identified if a large number of growth stages or size classes were used to produce the age structure; inconsistent mortality and fecundity would produce a number of peaks and

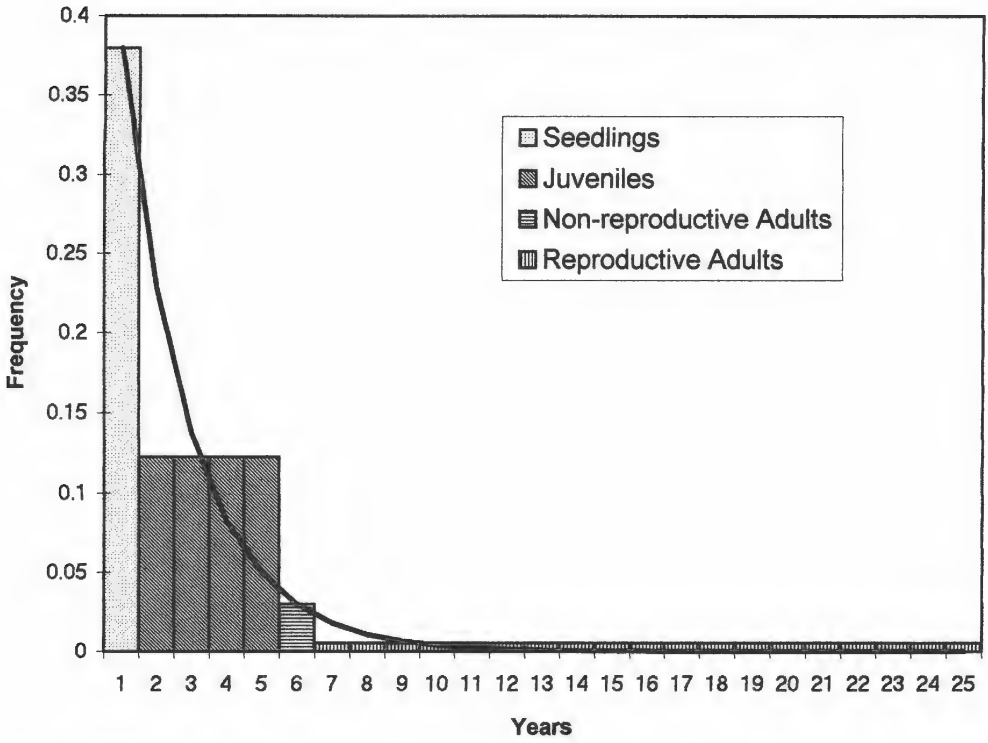

Figure 4. Hypothesized age structure for *Corydalis aquae-gelidae* on the Mt. Hood National Forest. From a sample of 2615 plants throughout the Mt. Hood National Forest. The curve was produced by the exponential decay function: frequency = 0.6314 exp (-0.5078 year), which was fitted to the histogram data.

valleys in the age structure. *Corydalis aquae-gelidae* appeared to fit this requirement of consistency; all plants with 14 or more leaves flowered, many seedlings were observed during both study years, and the age structure showed a monotonic decline.

Plant Strategies

Grime (1979) predicts that plants of relatively resource-poor environments will be intrinsically slow-growing, with high allocation to storage, rather than reproductive or resource-gathering organs. *Corydalis aquae-gelidae* had the relatively high root/shoot ratio (about 2.4-3.8, table 3) and low reproductive allocation of a stress-tolerator (about 8%). Apparently, most of the photosynthate produced by seedlings their first year is stored as starch in the tuberous root; seedlings rarely produced any true leaves their first year. These allocation patterns would lead to a high root/shoot ratio. Many other plants have relatively less biomass allocation to belowground structures. For example, eight perennial Compositae and Umbelliferae species had a mean belowground/aboveground biomass ratio of 0.74 (range 0.22 to 2.89, Lovett-Doust 1980, Abrahamson and Caswell 1982); rhizomes were included with roots. Harper (1977) suggests that herbaceous perennials allocate 5 to 25% to reproduction.

Corydalis aquae-gelidae also had the comparatively slow growth and long non-reproductive period of a stress-tolerator. Shade-tolerant temperate forest herbs cited by Bierzychudek (1982) require one to ten years for first reproduction; *Corydalis*, at 7 years (or between 6 and 9 years) according to the growth model, was at the high end of this range. *Corydalis* was generally found

in cold, wet, shaded conditions, with a coarse, mineral substrate, i.e., relatively unproductive habitats. Catastrophic disturbances during floods are relatively infrequent in *Corydalis aquae-gelidae* habitat (Goldenberg 1992).

Management Implications

The results imply that *Corydalis aquae-gelidae* populations would not rebound vigorously after disturbance, due to its slow growth and a long pre-reproductive period. Disturbance due to land management would, instead, favor more ruderal or competitive species. Ruderal species are fast-growing species with high reproductive allocation, while competitive species are fast-growing, but with allocation to continued vegetative growth (Grime 1979). Preservation of the habitat should be adequate for preserving the species, however. Human intervention seems unnecessary, as the populations appear to be reproducing successfully, as based on the estimated age structure.

Corydalis aquae-gelidae is generally considered to be associated with late-successional or old-growth forest (USDA-FS, USDI-BLM 1994), and this work confirms that view. Grime (1979) considers that stress-tolerant plants are typical of late-successional forest understories. These plants must tolerate deep shade and a lack of free nutrients. Disturbance due to fire or timber harvest would increase available sunlight and nutrients, and should favor other species.

Acknowledgements

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Seasonal Variation in Glutathione Reductase Activity in Coastal and Montane Populations of Lodgepole Pine (*Pinus contorta*)

Abstract

Increased activity of antioxidant defense enzymes, such as glutathione reductase (GR), is one mechanism employed by plants to prevent oxidative damage during low-temperature stress. Lodgepole pine (*Pinus contorta* Dougl.) was chosen to test the hypotheses that 1) enhanced GR activity would accompany cold acclimation and 2) montane populations (*P. contorta* var. *latifolia*) would have a higher level of GR activity than coastal populations (*P. contorta* var. *contorta*). Seasonal changes in specific activity of GR in needles of *P. contorta* were monitored in montane and coastal populations. Greenhouse and growth chamber experiments were performed to investigate the effect of temperature on GR activity and total glutathione content. Glutathione content and specific activity of GR were consistently higher in the montane site than in the coastal site during the winter. GR activity peaked at the onset of freezing low temperatures in the montane population but soon decreased again despite the persistence of freezing temperatures. Seedlings exposed to low temperatures in a growth chamber had higher levels of GR activity than did comparable seedlings maintained under higher temperatures, however, total glutathione was similar for both treatments. These data suggest that GR and glutathione may play a central role in cold acclimation especially during early phases and that these factors account in part for the considerable cold tolerance of lodgepole pine.

Introduction

Antioxidant defense systems are an important component of cold acclimation in plants (Guy 1990; Kuroda et al. 1991). As temperatures decrease with the onset of winter, the rate of the temperature-dependent enzymatic reactions of metabolism, including the carbon-fixing Calvin cycle of photosynthesis, slows. However, the temperature-independent light-harvesting Hill reactions continue to supply high-energy electrons to the metabolic pathways of the cell at a constant and relatively high rate. The reduced energy demands of the plant's slowed metabolism can no longer provide a sufficient acceptor pool for these electrons, which may instead reduce oxygen, leading to the formation of oxygen radicals (Scandalios 1990). Thus, colder temperatures promote an abundance of oxyradicals in the tissues of the plant, and the activity of the antioxidant defense system is necessary to degrade these potentially damaging oxygen species.

The initial oxygen free radical and the source of other oxyradical species in plants is the superoxide radical ($O_2^{\cdot-}$). In the first step of the ascorbate peroxidase-glutathione reductase antioxidant defense pathway (Dalton 1995), superoxide disproportionates to hydrogen peroxide in a reaction catalyzed by superoxide dismutase. Hydrogen peroxide is then reduced to water by ascorbate peroxidase in a reaction coupled to the oxidation of ascorbate to form monodehydroascorbate. Monodehydroascorbate is further oxidized to dehydroascorbate, which is then reduced back to ascorbate by dehydroascorbate reductase in a reaction coupled with the oxidation of glutathione (GSH) to its oxidized form (GSSG). In the final step of the pathway, GSSG is recycled back to GSH by NADPH-dependent catalysis with glutathione reductase (GR; EC 1.6.4.2). Thus, this pathway provides a mechanism for detoxification of oxygen radicals, including those produced during low-temperature stress. Those species best able to neutralize oxyradicals produced during photooxidative stress associated with cold acclimation are at a competitive advantage in low-temperature environments.

Photooxidative stress in cold acclimation is of particular importance for evergreen coniferous species, which retain their photosynthetic apparatus throughout the winter. Several studies have confirmed the role of antioxidant defense in cold acclimation in species of conifers recognized as cold-tolerant. Anderson et al. (1992) reported increases in activity and substrates of the enzymes of the ascorbate-glutathione pathway during the winter months in needles of eastern white pine (*Pinus strobus*), with the peaks disappearing again during the summer. A similar response has been

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well-documented in spruce (*Picea rubens* and *P. abies*, Hausladen and Alscher 1994; Doulis et al. 1993; Madaminchi et al. 1990). The primary role of GR in preventing photooxidative stress is indicated by the observation that approximately 80 % of all GR in photosynthetic cells is located in the chloroplasts (Anderson et al. 1990).

Lodgepole pine (*Pinus contorta*) is an interesting study species for the investigation of the role of antioxidant defense in cold acclimation. This species is one of the most diverse both in terms of geographical distribution (northern Canada to Baja California, Pacific coast to South Dakota) and environmental tolerance (Critchfield 1980). Variously characterized as drought-tolerant (Sorenson 1992), flood-tolerant (Youngberg and Dyrness 1959), and cold-tolerant (Sorenson and Miles 1974), *P. contorta* thrives in a variety of harsh environments. Four varieties (or subspecies) have been recognized on the basis of morphology, and more recent molecular studies have supported this taxonomic arrangement (Wheeler and Guries 1982). Of these varieties, var. *contorta* (shore pine) occupies the coastal areas (Alaska to California) of the species range. Variety *murrayana* predominates in the Cascade Mountains of Oregon (Wheeler and Guries 1982), but var. *latifolia* extends into the northern Oregon Cascades and some authorities (Hitchcock and Cronquist 1974) place all non-coastal *P. contorta* within this latter variety. This article uses the *latifolia* nomenclature. The varieties of *P. contorta* display marked morphological differences, which are accompanied by physiological distinctions in lignification (Hagner 1970), monoterpene composition (Forrest 1980), and photosynthetic rate (Lopushinsky 1975). Since the maritime habitat of var. *contorta* experiences milder winter temperatures than the higher-elevation range of var. *latifolia* and few tree species can match this range of environmental tolerance, *P. contorta* is ideal for the study of the effect of temperature on the antioxidant defense systems of evergreen conifers.

This study examined the role of GR, as the terminal enzyme in the ascorbate-glutathione antioxidant defense pathway, in the freezing tolerance of *P. contorta*. Seasonal activity of GR was compared in geographically distinct populations of var. *contorta* (coastal provenance) and *latifolia* (montane provenance) to test the hypothesis that the latter, being exposed to colder winter temperatures, would exhibit consistently higher activity of GR and higher levels of glutathione. The hypothesis that lower temperatures result in increased levels of antioxidant activity was tested both by regression analysis of the relationship between temperature and GR activity in field experiments and by temperature-controlled experiments on seedlings of var. *contorta* maintained in a growth chamber.

Materials and Methods

Study sites and field collection

Coast site. The study population of shore pine (*Pinus contorta* var. *contorta*) was located on the Oregon coast at the Sand Lake recreational area of the Hebo Ranger District in the northern portion of the Siuslaw National Forest (45° 16' 30" N 123° 57' 00" W). The site was located within 10 m of sea level approximately 800 m inland from the shore zone. Two samples were taken from each of 3 trees within a 25-m radius of each other. Each tree had a height of 6-7 m and a dbh of 70-100 cm .

Montane site. The study population of lodgepole pine (*Pinus contorta* var. *latifolia*) was located in the White River drainage on the southern side of Mount Hood (45° 22' 00" N 121° 42' 30" W), at an elevation of approximately 1070 m. The site was approximately 200 m south of the junction of U. S. Highway 26 and Oregon State Route 35. Two samples were taken from each of 3 trees within a 25-m radius of each other. Each tree had a height of 10-11 m and a dbh of 70-100 cm .

Sample collection. Each site was visited every two weeks in the fall, beginning in the second week of October 1995. No needles were collected between the second week of December 1995 and the third week of January 1996. Beginning in the third week of January 1996, collections were made at monthly intervals. Needles were collected from each of the three study trees on each visit. Collection was consistently carried out during the noon hour. Needles were removed from the distal branch ends at breast height in a circuit around the entire tree, frozen in liquid nitrogen, and stored on dry ice for transport back to the lab. Specific activity of GR was monitored throughout the season in the field study, while glutathione content was determined only for the final collection date in each site.

Meteorological data. Values for daily high and low temperatures were obtained from the USFS "Cedar" weather station on the south side of Mount Hebo for the coast site and from the Government Camp weather station for the Cascade site. Temperature values used in regression analyses were means of daily high or low temperatures for the two weeks preceding the collection date.

Glutathione reductase assay. One-gram samples of needles were weighed, cut into 1-2 mm segments with a razor blade, and frozen in liquid nitrogen. Frozen needles were crushed with mortar and pestle and then macerated in 5 ml extraction buffer (50 mM Pipes, 6 mM L-cysteine, 10 mM D-isoascorbate, 1 mM EDTA, 0.3% Triton X-100, 1% PVP-10 and 1% Polyclar-AT), pH 6.8 (Anderson et al. 1990, 1992). This mixture was poured off and the remnants were rinsed from the mortar with another 5 mL of extraction buffer. Extracts were centrifuged at 20,000 g for 15 minutes at 4° C. The resultant supernatant was assayed spectrophotometrically for GR activity by monitoring the decrease in A_{340} due to GSSG-dependent oxidation of NADPH. Assays were performed at 25° C in a 1 mL-reaction mixture consisting of 0.25 µmol GSSG and 0.125 µmol NADPH in a buffer of 50 mM Tris-HCl (pH 7.8) plus 0.2 mM EDTA (Dalton et al. 1986), to which was added 50 µL of crude extract. Controls consisted of a non-enzymatic treatment (no enzyme added) and an assay for NADPH oxidase activity (no GSSG added). Activity units were defined as nmol NADPH oxidized per min. Activity was expressed as units · mg protein^{-1} or units · g FW^{-1}.

Protein determination. Protein content of crude extracts was determined by the method of Bradford (1976) using BSA as the standard.

Glutathione assay. Needle samples weighing 0.175 g were cut into 1-2 mm segments and placed in a 2.0 mL flat-bottomed Eppendorf tube with 1 mL of 5 % sulfosalicylic acid. The samples were thoroughly macerated with a Tissumizer (Tekmar TR-5T). Tubes were then microfuged at full speed for 5 min. The supernatant was removed and analyzed for total glutathione equivalents (GSH and GSSG) with a spectrophotometric assay based on the reduction of 5,5'-dithio-bis(2-nitrobenzoic acid) in the presence of excess glutathione reductase (Griffith 1980). Assays were performed at 25° C in a reaction mixture consisting of 300 µL 143 mM potassium phosphate buffer with 6.3 mM Na-EDTA (pH 7.5), 350 µL NADPH (0.496 mg · mL^{-1}), 100 µL distilled H_20, 100 µL 6 mM 5,5'-dithio-bis-2-nitrobenzoic acid (DTNB), 50 µL 5% sulfosalicylic acid, and 50 µL extract. The above reagents were added to the cuvette in a 32° C water bath, and the reaction was initiated with the addition of 50 µL yeast GR (Sigma) at a concentration of 10 units/mL. GSSG content was determined after derivitization of 250 µL of the above extract with 5 µL of 2-vinyl pyridine and 20 µL of 50% (v/v) triethanolamine. For field extraction, a 2.0 µL flat-bottomed Eppendorf tube was filled to the 0.5 mL mark with segmented needles, and 1.0 mL 5% sulfosalicylic acid was added. The tubes were then placed on dry ice for transport back to the lab, where their contents were thawed and extracted as above.

Greenhouse and growth chamber experiments. One hundred 2-year old seedlings of shore pine (*P. contorta* var. *contorta*) were obtained from D. Wells Farms (Aurora, OR). Seedlings were grown from seed stock originating from the central coast of Oregon. The seedlings were removed from the field and transported to Reed College between 14 Feb. and 21 Feb. Seedlings were individually potted in vermiculite in 6-inch pots and watered daily. Nutrients were supplied via irrigation with modified Hoagland's solution once per week (Jiang et al. 1989). Photoperiod was 16 h, with a thermoperiod of 32° C days/19° C night. Halide lights provided a photon flux density at seedling height of 300-400 µE · m^{-2} · s^{-1}. After two weeks in the greenhouse, 20 seedlings were chosen at random and transported from the greenhouse to a Percival Model MB60-B Plant Growth Chamber to induce cold acclimation response. Photoperiod in the growth chamber was 11 h, with a thermoperiod of 13° C day/ minus 4° C night. The photon flux density was 35 µE · m^{-2} · s^{-1}. Needles were collected from seedlings in the greenhouse (GH) and the growth chamber (GC) at weekly intervals beginning one week after potting. Specific activity of GR and glutathione content were determined at each collection. The new flush of needles began appearing on the GH seedlings approximately three weeks after arrival, and by the sixth week were abundant enough for collection and analysis as a third treatment.

Results

Seasonal Trends in GR Activity

GR activity in extracts from needles from the montane site (var. *latifolia*) showed a 2.3 -fold

increase between the collection dates of 27 Oct. and 10 Nov. (Figure 1). Residual plots showed no evidence of non-normalcy or non-constant variance and thus met the assumptions for use of ANOVA. A one-way ANOVA for the entire sampling period showed a significant effect ($F = 9.187$, $p < 0.0001$) of collection date. GR remained elevated through the 27 Nov. sampling, but then returned to previous levels for samples collected from 8 Dec. to 27 March. The overall mean of GR activity for all dates was 210 units · mg protein^{-1} or 214 units · g needle FW^{-1}. This seasonal pattern was essentially identical regardless of whether activity was expressed on a protein basis or a FW basis.

In contrast, GR activity in extracts from needles from the coastal site (var. *cortorta*) remained relatively unchanged throughout the sampling period (Figure 1, 3 Nov. - 1 Apr.). A one-way ANOVA for the entire sampling period showed no significant effect ($F = 1.428$, $p = 0.2327$) of collection date. The overall mean of GR activity for all dates was 112 units · mg protein^{-1} or 116 units · g FW^{-1}. The activity of coastal extracts was consistently below activity of montane extracts, however these differences were significant only for samples collected in November, where GR activity in montane samples was 3.0 -fold higher than activity in coastal samples. One-way ANOVA analysis of GR activity (all dates)

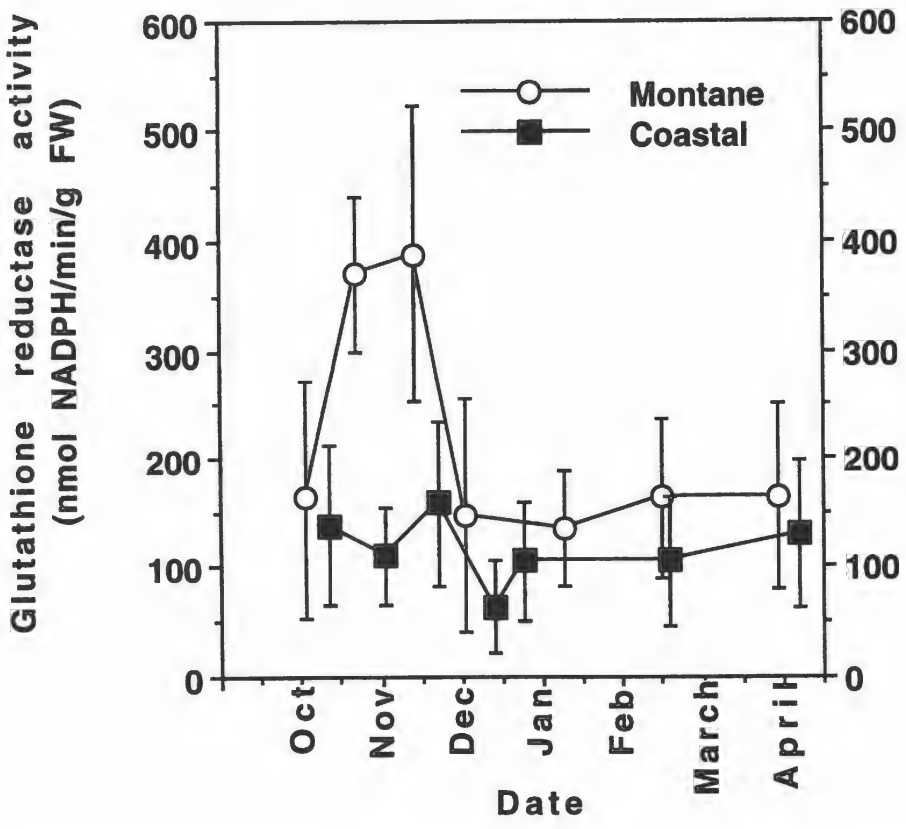

Figure 1. Glutathione reductase activity in extracts from needles of *P. contorta* var. *latifolia* (montane) and *P. contorta* var. *contorta* (coastal) over the course of the collection period (27 October 1995 - 1 April 1996). Each value is the mean of 6 trials (2 replicates from each of 3 trees); error bars show 95% confidence intervals.

indicated a high level of significance between GR activity at the 2 sites ($p<0.0001$).

Correlation of GR activity with temperature in field sites. At the montane site, the increase in GR activity from the first collection date to the second was accompanied by the first drop below freezing low temperatures. Regression analysis for all sampling dates at the montane site revealed a significant relationship between GR activity and mean low temperatures in the 2-week period preceding sampling ($p = 0.0175$, $r^2 = 0.116$). No significant relationship was found between temperature and GR activity at the coastal site.

Glutathione content. Glutathione content was assayed only on the final collection date at each site. Levels of oxidized glutathione were too low to be detected, but it was possible to estimate the total glutathione content (both oxidized and reduced forms) in the needles. Total glutathione content was significantly greater (unpaired t-test: $p = 0.0031$) in needles of trees at the montane site (24.2 $\mu mol \cdot g\ FW^{-1}$) than in those at the coast (15.0 $\mu mol \cdot g\ FW^{-1}$).

Greenhouse and grown chamber experiment. Specific activity of GR in extracts from needles of GH seedlings displayed a steady decline from the time the seedlings were placed in the greenhouse until the end of the experiment, evident as a significant effect of collection date on GR activity in the GH treatment (one-way ANOVA: $F = 10.177$, $p = 0.0005$). There was no similar significant effect of date on GR activity in GC seedlings (one-way ANOVA: $F = 0.476$, $p = 0.7075$). GH and GC needles from any one date (8 Mar. through 29 Mar.) did not have significant differences. However, if values for all above dates were combined GR activity was significantly higher (unpaired t-test: $df = 22$, $t = 2.907$, $p = 0.0082$) in extracts from needles of seedlings from the GC treatment than in those in the GH (Figure 2).

New needles became abundant enough for collection from GH seedlings by the 29 Mar. collection date. GR activity in extracts from new needles of the GH seedlings was significantly higher (unpaired t-test, $p = 0.0114$) than in those from their older counterparts (Figure 2).

Glutathione content was assayed in old needles of both GC and GH seedlings beginning on the 8 Mar. collection date, when seedlings were first placed in the GC. There was no significant difference (unpaired t-test, $p = 0.8473$) between extracts from the GH and GC in total glutathione content over the entire course of this experiment (Figure 3). On the final collection date, glutathione content was also assayed in the new needles of the GH treatment, which displayed significantly higher (Mann-Whitney U-test: $U = 9$, $Z = 1.964$, $p = 0.0495$) total glutathione content than the older needles of the same treatment (Figure 3).

Discussion

The finding that GR activity over the winter was significantly higher in the montane population (var. *latifolia*) than in the coast population (var. *contorta*) is in keeping with the initial hypothesis that those individuals in a location subjected to longer intervals of freezing would have higher levels of GR activity to counteract the harmful effects of photooxidative stress associated with chilling. It is unlikely that cold temperatures are the only factor influencing levels of GR activity in the needles of *P. contorta*. Though these experiments provided no platform for assaying genetic differences between varieties, it is certainly possible that different isoforms of GR with different temperature optima might exist between or within varieties. GR isoforms specific to cold-hardened and nonhardened needles have been identified in red spruce (Doulis et al. 1993; Hausladen and Alscher 1994).

The lack of variation in GR activity in needles of var. *contorta* at the coast site over the course of the winter suggests either that the environmental cues which would trigger an increase in activity levels were absent at the site, or that such a response is not present in that variety. As no prolonged periods of nightly freezing occurred at the coast site, it is more reasonable to adopt the former as the more conservative explanation. Anderson et al. (1992) offer a similar rationale for *Pinus strobus*, in terms of fewer degree hours below 5° C, to account for reduced activity levels of GR in a study site which had exhibited high levels in the previous year.

The pronounced peak in GR activity at the montane site confirms the expectation that GR activity increases in response to low-temperature stress. However, in contrast to the report of Anderson et al. (1992) on *P. strobus*, the peak occurred early in the winter, well in advance of the prolonged interval of freezing low temperatures. One

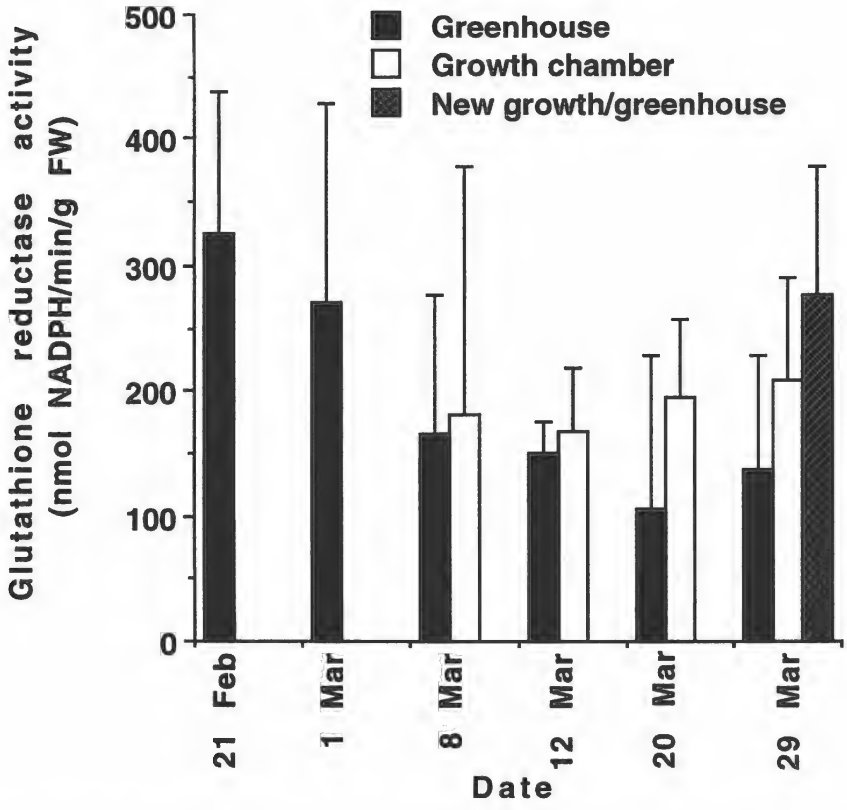

Figure 2. Glutathione reductase activity in extracts from needles of *P. contorta* var. *contorta* seedlings over the course of the temperature-controlled experiments (21 Feb. 1996 - 29 March 1996). The greenhouse thermoperiod (day/night) was 32° /19° C and the growth chamber thermoperiod was 13° /-4° C. Each value is the means of 6 trials (2 replicates from each of 3 trees); error bars show 95% confidence intervals.

possible explanation for our observations between GR activity levels, time of year, and temperature would involve an initial increase of GR activity during cold acclimation followed by a decrease with the onset of winter dormancy. Havranek and Tranquillini (1995) review a number of cellular alterations leading to reduced light-harvesting as a result of cold acclimation in conifers, including reduced cytochrome and chlorophyll content of the thylakoid membranes, clumping and migration of chloroplasts to light-protected regions of the cell, and increased opacity of the cytoplasm due to vacuolar fragmentation. The carbon fixation pathways of photosynthesis stop abruptly upon initial formation of ice in plant tissues (Larcher 1995), but the physical rearrangement of cellular components probably occurs over a longer time frame, necessitating an intervening protective mechanism. Assuming that similar cytological rearrangements occur during cold acclimation of *P. contorta*, a scenario can be envisioned in which GR activity increases early in acclimation to protect the thylakoid membranes from photooxidative damage, but declines as the light-harvesting apparatus is sequestered.

As var. *contorta* exhibited no response to low temperature in field conditions, the opportunity to subject seedlings of that variety to freezing low temperatures was of interest. The higher levels of GR activity in needles of the GC treatment support the hypothesis that low-temperature stress triggers an increase in the activity of antioxidant defense enzymes even in var. *contorta* which would not normally be exposed to conditions of low temperature.

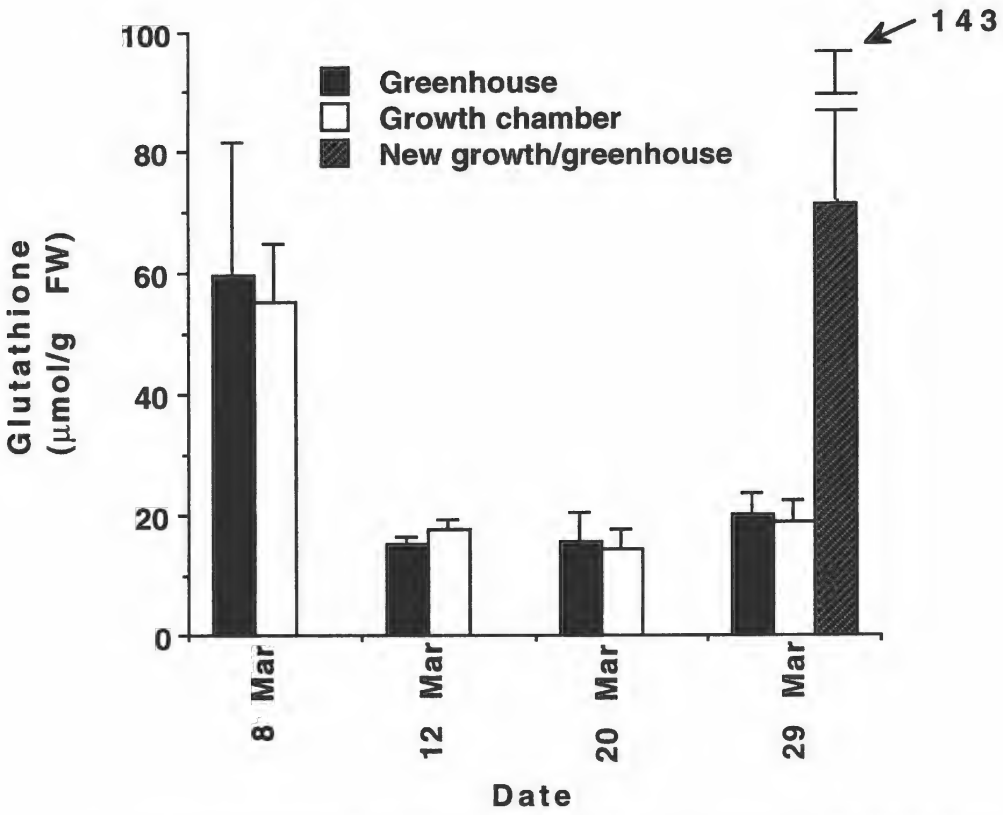

Figure 3. Total glutathione (oxidized + reduced) content in extracts from needles of *P. contorta* var. *contorta* seedlings over the course of the temperature-controlled experiments. Thermoperiod was as described in Fig. 2. Each value is the mean of 6 trials (2 replicates from each of 3 trees); error bars show 95% confidence intervals.

The greater mean total glutathione content in needles of trees at the montane site agrees with reports of higher glutathione content in red spruce in response to winter conditions (Madaminchi et al. 1990). A more informative measure would have been the ratio of reduced to oxidized glutathione, however, levels of oxidized glutathione were too low to detect despite the high sensitivity (low nmolar range) of the assay. Thus, it appears that GR was operating with high efficiency in all cases.

Pinus contorta is one of the most ecologically tolerant of conifer species. This species is found at elevations from sea level to over 3,300 m and in habitats with annual rainfall from 27 to over 150 cm. It displays a remarkable tolerance to extreme edaphic situations, including wet, droughty, or infertile soils (reviewed by Lotan and Perry 1983) although the physiological mechanisms responsible for this environmental resiliency are not clear. Ability to withstand extreme cold can be attributed in part to a number of factors to reduce light-harvesting (reviewed by Havranek and Tranquillini 1995). These mechanisms for reduction in light harvesting are advantageous in times of stress because the plants' diminished capacity for CO_2 fixation results in a lowered photon-utilizing capacity and a tendency for reduced intermediates of the light reactions of photosynthesis to produce harmful activated forms of oxygen such as superoxide, H_2O_2, and hydroxyl radicals (reviewed by Asada 1996). Antioxidant defenses are extremely critical under such situations. Our studies suggest that such defenses are partly

responsible for the extreme cold tolerance of *Pinus contorta*. According to Sakai and Weiser (1973), *P. contorta* from Montana can withstand temperatures as low as -80 ° C. No other conifers in these authors' Pacific coast grouping is capable of surviving these extremes of cold. Furthermore, many Pacific Northwest conifers conduct a substantial part of their total annual photosynthesis during the winter (Waring and Franklin 1979). Enhanced antioxidant defenses may be an essential feature of these conifers that allows for this ability.

In conclusion, cold acclimation in *Pinus contorta* var. *latifolia* growing in a harsh montane climate involves elevated levels of glutathione and an initial increase in GR activity. This increase is not evident in individuals of *P. contorta* var. *contorta* growing in a more moderate coastal climate. Because numerous types of environmental stress (e.g., chilling, drought, heat, strong light, and xenobiotics) promote oxidative damage, it may be that the antioxidant defenses are a primary mechanism that explains the environmental tolerance of *Pinus contorta* as well as many other conifer species. Further studies are required to examine these possibilities.

Acknowledgements

Thanks are owed to the staffs of the Hebo Ranger Station, Siuslaw National Forest, and of the Supervisor's Office, Mount Hood National Forest, for permission to set up field sites on National Forest lands, as well as to the Oregon State University Climatology Office and John Kwait of the Oregon State University Fire Management Service, for meteorological data.

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Winter Ecology of Bald Eagles in the Nisqually River Drainage, Washington

Abstract

We studied the winter ecology of a population of bald eagles (*Haliaeetus leucocephalus*) on the Nisqually River and a tributary, Muck Creek, in Washington, for 3 years. Peak eagle numbers on the river and creek combined occurred in early February and were 168 in 1991-92, 128 in 1992-93, and 156 in 1993-94. For the 3 years, 79% of eagles used the Nisqually River and 21% used Muck Creek. Eagle use of the river was high between 8 and 18 km (5 and 11 miles) upstream of Puget Sound and at the mouth of Yelm Creek; use on Muck Creek was concentrated on the lower 4 km (2.5 miles). The subadult proportion in the study area was 46% in 1991-92, 41% in 1992-93, and 43% in 1993-94; it increased throughout each winter; and it was higher where most eagles congregated. Chum salmon (*Oncorhynchus keta*) was the primary food source, and this eagle population was predicted to consume 1,100 salmon carcasses each winter based on the yearly average of 6,952 eagle use days on the river and creek. Black cottonwood (*Populus balsamifera*) was the most widely used tree species by both perching (53% of 1,423 eagle sightings) and roosting (53% of 94 roost trees) eagles, and 8 of 9 communal roosts were located in old-growth forests. Management to enhance chum salmon runs, maintain forest habitat, and regulate human disturbance is needed to protect this eagle population.

Introduction

Washington has the largest number of wintering bald eagles in the contiguous United States (Stalmaster 1987:31), and most of these eagles use rivers in the western portion of the state. Large winter populations of eagles in Washington exist on the Skagit River (Servheen 1975, Ralph 1980, Stalmaster 1989, Hunt et al. 1992), Sauk and Suiattle rivers (Russell 1980, Stalmaster 1989), Nooksack River (Stalmaster et al. 1979, Knight and Knight 1983), Skykomish River (Hansen and Bartelme 1980), Lewis River (Anderson and Ichisaka 1986), and Columbia River (Fitzner and Hanson 1979, Knight et al. 1979, Fitzner et al. 1980, Wood 1980, Fielder and Starkey 1980, 1987). A wintering eagle population on the Nisqually River and its tributaries has been locally known for years (Harrington-Tweit and Kerwin 1979, 1980; U.S. Army unpubl. data), but never studied in detail. The purpose of this study was to determine the numbers and distribution of bald eagles on the Nisqually River and Muck Creek, locate communal night roosts, document diurnal and nocturnal habitat use, and assess dietary habits.

Study Area

The study area is located south of Puget Sound and east of Olympia, Washington, mostly on the Fort Lewis Reservation (FLR), a U.S. Army Installation, and the Nisqually Indian Reservation (NIR) (Figure 1). The Nisqually River, which originates on Mount Rainier, traverses both reservations northward and empties into Puget Sound. Muck Creek traverses the FLR westward and empties into the Nisqually River 18 km (mile 11) upstream from Puget Sound. Yelm Creek passes through private land in the study area and enters the Nisqually River 21 km (mile 13) upstream from Puget Sound. Most shorelines of the river and creeks in the study area are undeveloped; the studied portion of Muck Creek flows through military firing ranges on the FLR.

The study area is in the *Tsuga heterophylla* (western hemlock) Vegetation Zone (Franklin and Dyrness 1973). Most forests on the FLR are composed of Douglas-fir (*Pseudotsuga menziesii*) and are managed for development of late successional stages. Forests on the FLR along the Nisqually River and Muck Creek are protected from harvest and some are old-growth. Riparian forests along the river and creek consist mostly of red alder (*Alnus rubra*), black cottonwood, Douglas-fir, big-leaf maple (*Acer macrophyllum*), western red cedar (*Thuja plicata*), and Sitka spruce (*Picea sitchensis*). Oregon white oak (*Quercus garryana*),

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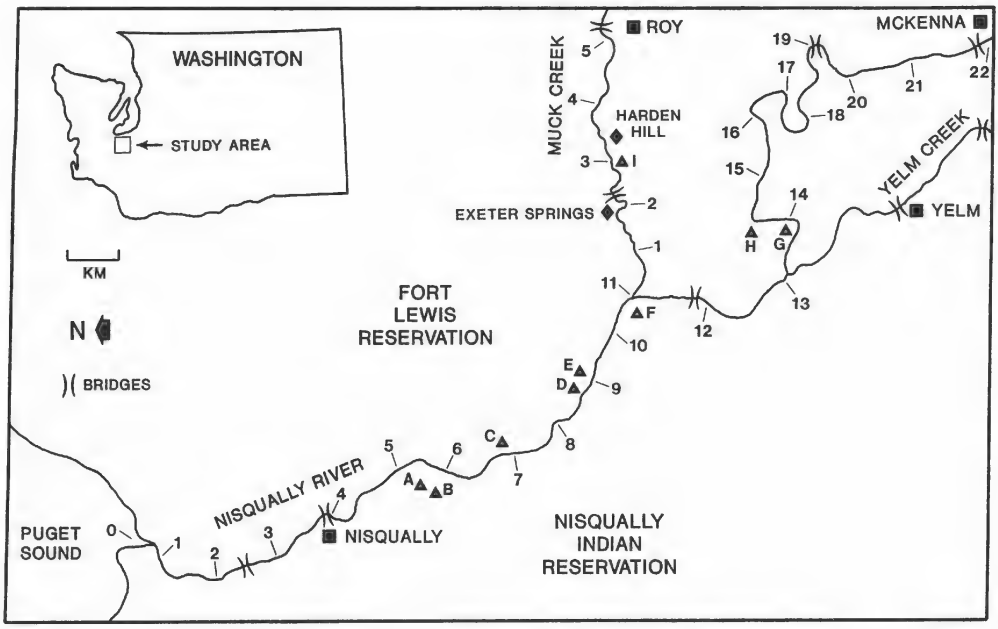

Figure 1. Map of the study area showing locations of the Nisqually River, Muck Creek, and Yelm Creek; numbers indicate river or creek mile designations. Locations of the 9 communal roosts (triangles) are also displayed (A = Tree Farm, B = Side-Channel, C = Carter Woods, D = Riverbend, E = Cabin Creek, F = Collard Woods, G = Yelm, H = Bluff, and I = Muck Creek).

grand fir (*Abies grandis*), shore pine (*Pinus contorta*), western hemlock, and snags of various species also exist.

Chum salmon spawn and die in the Nisqually River and Muck Creek. This chum salmon run is one of the latest in North America, with peak die-offs occurring in January and February, and as much as one-third of the run spawning in Muck Creek (Holler 1990). In droughty years, however, low instream flows can prevent salmon from entering the creek. Coho salmon (*Oncorhynchus kisutch*), steelhead trout (*O. mykiss*), and other salmonids also spawn in the drainage.

Methods

We made weekly counts of bald eagles on the Nisqually River by drifting in a raft from McKenna (river mile 22) to Nisqually (mile 4) (Figure 1). We conducted 20 censuses from November to April in 1991-92, and 16 from December to April in both 1992-93 and 1993-94. We conducted all censuses from 0900 to 1400 hours on weekdays. Of the 31% of eagles that were flushed by our raft and flew downstream, ca. 75% remained within view and thus were not counted again. Of the remaining ca. 25% of eagles that flew downstream and out of view, we recorded each as one-half of a sighting to minimize duplicate counts. We believe our counts were accurate within a 5% range of error for eagles perched <50 m from the river. We recorded eagle age and behavior, river mile location, and use of perch tree species for all sightings. Eagles with mostly white heads were recorded as adults, and brown and mottled eagles were recorded as subadults. We assessed diets of eagles on the river by identifying food carcasses seen eaten by eagles during censuses.

The percentage of the population composed of subadults was analyzed for weekly trends during all 3 years and in relation to eagle density along the river. We plotted subadult proportions by week over the winter season using linear regression weighted by weekly subadult percentages. Subadult proportions also were compared with the seasonal total number of eagles recorded per river mile using linear regression.

We counted eagles on Muck Creek from the confluence with the Nisqually River to 8.4 km (5.2 miles) upstream, using UH-1 Huey or OH-58 Bell helicopters, the best method for censusing this inaccessible area (Figure 1). We conducted 14 censuses from December to March in 1991-92, 11 in 1992-93, and 9 in 1993-94. We conducted all censuses in late morning on weekdays for <1 hour in duration. Flight speeds generally were 35 to 55 km/hour and altitudes were 60 to 120 m above ground. To prevent duplicate counts, all eagles that flushed and flew ahead of the helicopter were kept in continuous view. We believe, however, that our counts by helicopter underestimated actual eagle numbers (Stalmaster 1994). Eagle sightings were subdivided into upper, middle, and lower reaches of the creek using the Nisqually River (creek km and mile 0.0), the bridge near Exeter Springs (km 3.9, mile 2.4), Harden Hill (km 5.6, mile 3.5), and the bridge near Roy (km 8.4, mile 5.2) as dividing landmarks (Figure 1).

We found night roosts by visually following eagles in late afternoon using vantage points along the Nisqually River and Muck Creek. After roost locations were determined, we made weekly counts of eagles arriving at each roost from 1500 hours until dark. Guano on the ground indicated specific roost trees used by eagles.

We used eagle use days (EUDs) to assess eagle use on the study area (McClelland et al. 1982). EUDs, the area under a population curve, represent a combination of eagle numbers and the length of time that eagles are present and are calculated as follows:

$$EUDs = \Sigma\, Di(C_i + C_{i+1})/2$$

where D = number of days between counts i and i + 1, i = count number, and C = number of eagles per count. Similarly calculated, eagle use nights (EUNs) were used to document eagle use of night roosts.

Perch tree use on the Nisqually River was compared to tree availability to determine if eagles preferred or avoided specific tree species (Stalmaster and Newman 1979). We determined tree species availability by establishing 72 plots and sampling 288 trees >25 cm diameter within 50 m of both shorelines of the river from river km 6.5 to 34.6 (mile 4.0 to 21.5), using the point-centered quarter method (Lindsey et al. 1958). We used X^2 2 x 2 contingency tables to determine statistical significance of tree species preference or avoidance. We recorded species and health of trees at communal roosts, and measured representative trees for height (clinometer) and diameter at breast height (measuring tape).

Results and Discussion

Population Dynamics

Bald eagles wintered on the Nisqually River (Figure 2) and Muck Creek (Figure 3) primarily from late December to late March; weekly high counts on the river and creek combined were 168 in 1991-92, 128 in 1992-93, and 156 in 1993-94. Eagle numbers on the Nisqually River were high in 1993-94 compared to other years and numbers peaked between late January and late February, depending on the year. High counts on the river were 105 in 1991-92, 83 in 1992-93, and 155 in 1993-94. In contrast, eagle numbers on Muck Creek were exceptionally low in 1993-94 compared to other years, but peak counts were all recorded in early February. High counts on the creek were 77 in 1991-92, 60 in 1992-93, and 10 in 1993-94.

We recorded a 3-year average of 6,952 EUDs on the study area; 7,036 in 1991-92, 6,452 in 1992-93, and 7,367 in 1993-94 (Table 1). For the 3 years combined, 79% of EUDs were on the Nisqually River and 21% on Muck Creek. During 1991-92 and 1992-93, however, 70-71% of EUDs were on the river and 29-30% on the creek, compared to 1993-94 when 95% of EUDs were on the river and only 5% on the creek. Low eagle use on Muck Creek and higher use on the Nisqually River in 1993-94 were attributable to the low instream flows in Muck Creek which prevented salmon from entering the creek. These low flows were caused by unusually droughty weather and flows did not increase until mid-March, after the salmon spawning season.

The eagle population on the Nisqually River and Muck Creek (peak of 168 eagles) apparently is the fourth largest riverine concentration in Washington. Larger populations exist only on the Skagit River and its tributaries the Sauk, Suiattle, and Cascade rivers (peak count of 501 eagles, Stalmaster 1989), Nooksack River (peak of >200 eagles, Knight and Knight 1983), and Columbia River (Fielder and Starkey 1980, 1987).

Seventeen eagle counts by helicopter on the Nisqually River (river km 0-18, miles 0-11) and

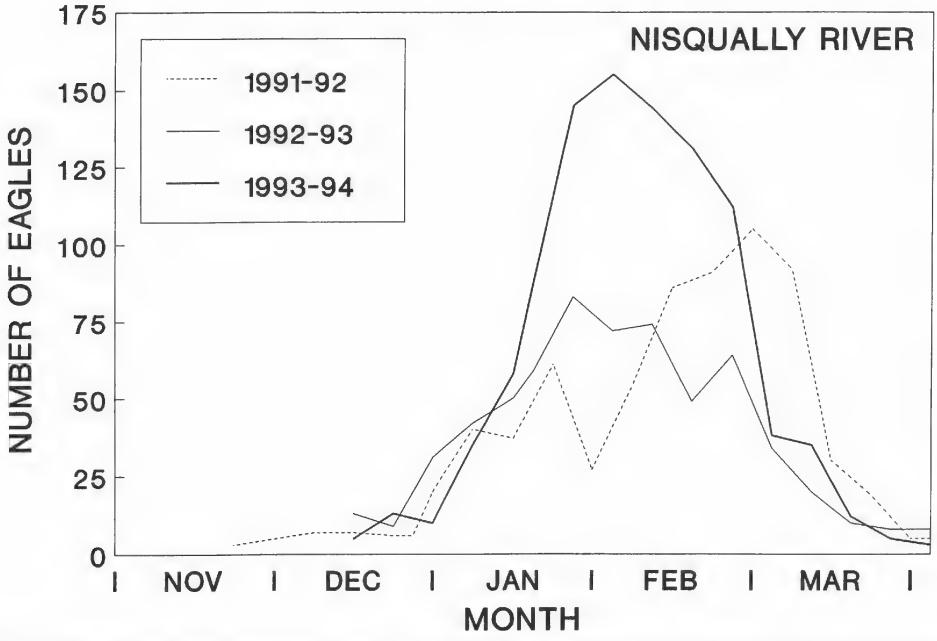

Figure 2. Numbers of bald eagles counted on 29 km (18 miles) of the Nisqually River by boat between McKenna and Nisqually during the winters of 1991-92, 1992-93, and 1993-94.

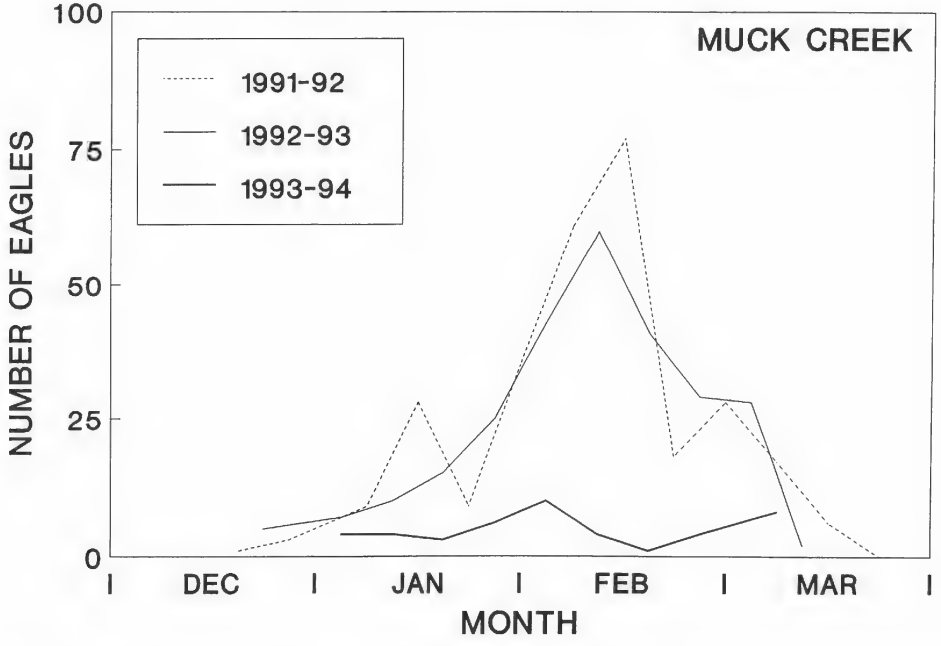

Figure 3. Numbers of bald eagles counted on the lower 8 km (5 miles) of Muck Creek by helicopter during the winters of 1991-92, 1992-93, and 1993-94.

TABLE 1. Mean number of eagle use days (EUDs) on the Nisqually River and Muck Creek during the winters of 1991-92, 1992-93, and 1993-94.

Location	1991-92		1992-93		1993-94		Means	
	EUDs	%	EUDs	%	EUDs	%	EUDs	%
Nisqually River	4,943	70.3	4,568	70.8	7,001	95.0	5,504	79.2
Muck Creek	2,093	29.7	1,884	29.2	366	5.0	1,448	20.8
Totals	7,036	100.0	6,452	100.0	7,367	100.0	6,952	100.0

Muck Creek (creek km 0-8, miles 0-5) in January or February from 1981 to 1991 averaged 24 eagles and ranged from 2 to 56 eagles (U.S. Army unpubl. data). We believe 4 factors explain why our high count (168) was 3-fold higher than the highest historic count (56): (1) instead of using a helicopter, our river censuses were conducted by boat which is a more thorough and accurate means of counting eagles (Stalmaster 1994), (2) our counts included a longer time span and always included February when peak numbers typically occurred, (3) we censused 29 km (18 miles) of river compared to 18 km (11 miles) by the U.S. Army, and (4) we speculate that there has been an increase in the eagle population.

Subadult Proportion

The subadult proportions on the Nisqually River and Muck Creek combined increased at similar rates during all 3 winters (Figure 4). This seasonal increase in the subadult proportion is explained by the early departure of adults to breeding areas in conjunction with the lateness of the salmon run and, therefore, the lateness of the eagle population.

The 46% subadult proportion on the Nisqually River and Muck Creek combined in 1991-92 was higher (X^2 2 x 2 table, $P < 0.05$) than the 41% recorded in 1992-93 and 43% in 1993-94. For the Nisqually River, the 52% proportion in 1991-92 was higher (X^2 2 x 2 table, $P < 0.05$) than the 41% in 1992-93 and 43% in 1993-94. For Muck Creek, the 16% proportion in 1993-94 was lower (X^2 2 x 2 table, $P < 0.05$) than the 31% recorded in 1991-92 and 39% in 1992-93.

The high proportion of subadults on the river in 1991-92 (52%) occurred in conjunction with a shift in the population curve to late winter (Figure 2). Because subadults were proportionally more common in late winter (Figure 4), the subadult proportion was therefore higher in 1991-92. The low proportion of subadults on Muck Creek in 1993-94 (16%) was likely due to a lack of salmon in the creek. Subadults tend to be proportionally less common than adults at low-yielding feeding sites (Stalmaster 1987:83).

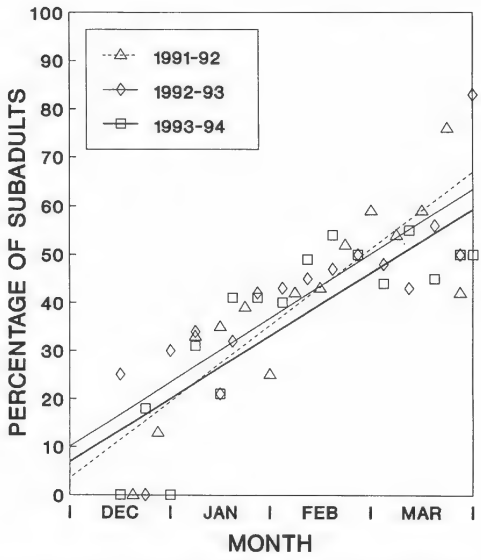

Figure 4. Relationship between the subadult proportion (Y) and week of season (X) during 3 winters on the Nisqually River and Muck Creek combined. Linear regressions were significant at $P < 0.001$ for 1991-92 ($n = 14$ weeks, $Y = 9.1 + 3.80X$, $r = 0.856$), 1992-93 ($n = 16$ weeks, $Y = 13.3 + 3.21X$, $r = 0.850$), and 1993-94 ($n = 16$ weeks, $Y = 10.2 + 3.13X$, $r = 0.833$).

Subadults were proportionately more common on Nisqually River reaches where eagles were most concentrated (Figure 5), on the lower reach of Muck Creek (36% subadults) where both food and eagles were most abundant compared to the

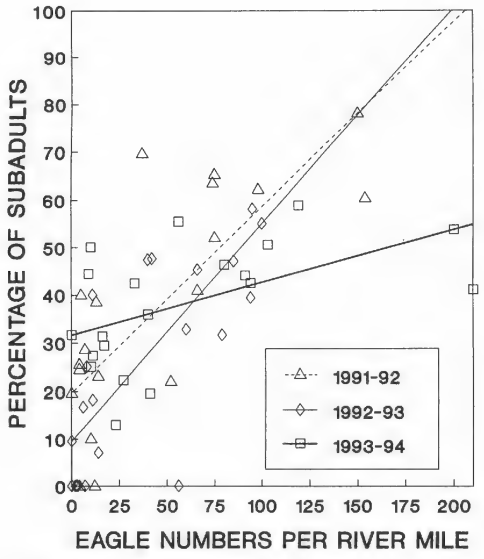

Figure 5. Relationship between the subadult proportion (Y) and total number of eagles counted during all censuses on 29 km (18 miles) of the Nisqually River (X) during each winter. Linear regressions were significant at $P < 0.001$ for 1991-92 ($n = 18$ censuses, $Y = 19.6 + 0.39X$, $r = 0.703$) and 1992-93 ($n = 17$ censuses, $Y = 10.8 + 0.44X$, $r = 0.774$), but not significant ($P = 0.061$) for 1993-94 ($n = 18$ censuses, $Y = 31.6 + 0.11X$, $r = 0.451$).

middle (32%) and upper (23%) reaches, and on the river (43%) instead of the creek (16%) in 1993-94 when low creek flows precluded spawning by salmon. Subadults are less adept at finding food than adults and more dependent on other eagles to find food (Knight and Knight 1983), and are therefore relatively more common in areas where the overall eagle population is high (Stalmaster 1987:83).

Distribution

Eagles congregated on the Nisqually River between river km 6 and 23 (miles 4 and 14); there were relatively few birds upstream of river km 23 (Figure 6) and few downstream of river km 6 (Stalmaster 1994). There was an average of 56% of eagle use between river km 8 and 18 (miles 5 and 11) during the 3 study years. Eagles were also common on km 21-23 (mile 13-14) (15% of total for 3 years) where Yelm Creek enters the river, and use on this stretch increased from 7% in 1991-92, to 15% in 1992-93, to 21% in 1993-94.

We believe that eagle distribution on the Nisqually River was primarily influenced by the availability of chum salmon carcasses, but riverine features, riparian habitat, and human activity also affected distribution. Where eagles were common, the river was wide, braided, and shallow

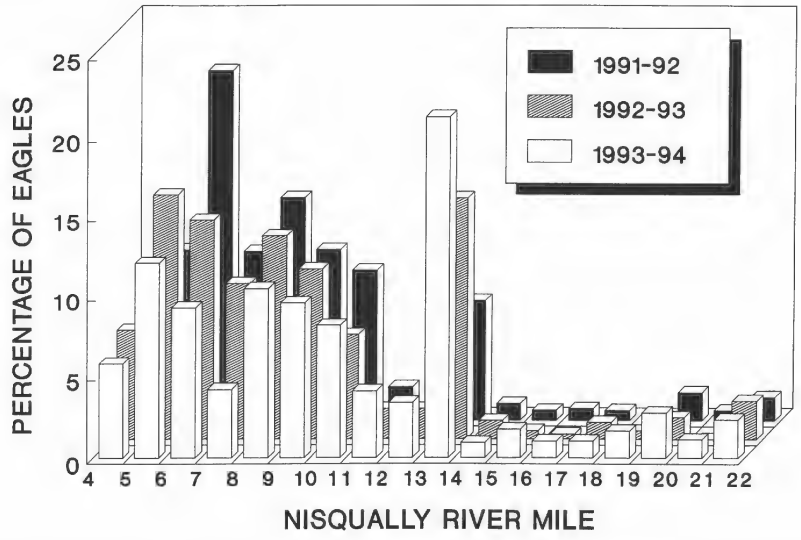

Figure 6. Distribution of bald eagles on 29 km (18 miles) of the Nisqually River during the winters of 1991-92, 1992-93, and 1993-94 (see Figure 1 for river mile locations).

which provided optimal salmon spawning habitat and caused stranding of carcasses. Tall, old-growth cottonwood trees often lined the banks where most eagles resided. Human presence also was generally low in areas of high eagle use. We speculate that the presence of numerous bank anglers on km 18-21 (miles 11-13) precluded normal eagle use of this river stretch (Stalmaster 1994). Also, eagles were common on the lower 1 km of Yelm Creek and along the adjacent river because they fed on a late winter salmon run in the creek.

On Muck Creek, 72% of eagle use was on the lower reach, compared to 15% on the middle reach and 13% on the upper reach. Feeding eagles were common near Exeter Springs (km 3.2, mile 2) in 1991-92 and 1992-93, where stream rehabilitation has enhanced chum salmon spawning habitat (Holler 1990).

Food Source

Of 118 eagles observed feeding on the Nisqually River, 75 prey items were identified: 72 (96%) chum salmon, and 1 (1%) coho salmon, black-tailed deer (*Odocoileus hemionus*), and hooded merganser (*Lophodytes cucullatus*). Although not quantified, chum salmon also was the primary food source on Muck and Yelm Creeks. Given an average of 6,952 EUDs for the study area (Table 1), a consumption rate of 0.49 kg salmon/bird/day (Stalmaster and Gessaman 1984), a 96% diet of chum salmon, a mean mass of 3.76 kg and a mean edible mass of 2.97 kg for each carcass (Stalmaster and Gessaman 1984, Stalmaster 1994), an estimated 1,100 chum salmon would be consumed by this eagle population each winter. Chum salmon is perhaps the single most important winter food of wintering bald eagles on rivers in the Pacific Northwest (Stalmaster 1987:94), and eagles on the Nisqually River, Muck Creek, and Yelm Creek are virtually dependent on this food source.

Roosts

We documented 6 traditionally-used, communal night roosts on the FLR and 3 on the NIR (Figure 1, Table 2). Using EUNs, Muck Creek was the largest roost (24% of use), followed by Carter Woods (22%), Cabin Creek (19%), and Yelm (18%). The highest nocturnal eagle counts were made at the Muck Creek roost in 1991-92 (68 eagles) and at the Yelm roost in 1993-94 (65 eagles).

TABLE 2. Peak bald eagle counts at 9 communal roosts on the study area during the winters of 1991-92, 1992-93, and 1993-94. Also presented are the mean number of eagle use nights (EUNs) during 1992-93 and 1993-94 combined.

	Winter			EUNs	
Roost	1991-92	1992-93	1993-94	Mean	%
Muck Creek[a]	68	36	22	1,107	24.2
Carter Woods[a]	27	26	16	984	21.5
Cabin Creek[a]	25	17	28	881	19.2
Yelm[a]	-	11	65	841	18.4
Side-Channel[b]	-	6	8	199	4.4
Bluff[a]	-	11	10	196	4.3
Tree Farm[b]	6	5	11	187	4.1
Collard Woods[b]	-	7	6	108	2.3
Riverbend[a]	-	-	8	74	1.6
Totals				4,577	100.0

[a]On Fort Lewis Reservation.
[b]On Nisqually Indian Reservation.

In 1993-94, Muck Creek roost counts were low because of a lack of salmon in the creek, and Yelm roost counts were high when a large run of salmon spawned in nearby Yelm Creek. Eagle use of the Carter Woods and Cabin Creek roosts was relatively consistent, and use at the other 5 communal roosts was low (each with <12 birds per night and <5% of total use). We found 10 other roosts that were used inconsistently by few birds (Stalmaster 1994).

Habitat Use

Black cottonwood was the most frequently used perch tree species (53%) on the Nisqually River, but red alder (18%) and Douglas-fir (11%) also were widely used (Table 3). Comparing perch use to availability, snags were strongly preferred, but black cottonwoods and big-leaf maples also were preferentially selected. In contrast, red alder and Douglas-fir were avoided by eagles, relative to their availability.

Eagles preferred diurnal perches that were (1) close to the shoreline and salmon carcasses, (2) tall with stout, horizontal branches that provided panoramic views, and (3) had open, unrestricted flight paths. Cottonwoods provided these characteristics thereby explaining why they were both frequently used and preferred by eagles. Preferred use of snags, cottonwoods, and maples in west-

TABLE 3. Perch type preferences of wintering bald eagles along the Nisqually River during the winters of 1991-92, 1992-93, and 1993-94.

Perch type[a]	Availability		Utilization		Ratio[b]	X^2
	n	%	*n*	%		
Snag[c]	2	0.7	77	5.4	7.7	451.2*
Black cottonwood	78	27.1	760	53.4	2.0	363.5*
Big-leaf maple	12	4.2	112	7.9	1.9	45.6*
Sitka spruce	2	0.7	14	1.0	1.4	1.6
Western red cedar	12	4.2	51	3.6	0.9	1.3
Oregon white oak	1	0.3	3	0.2	0.7	0.4
Douglas-fir	49	17.0	153	10.8	0.6	32.7*
Red alder	132	45.8	251	17.6	0.4	246.4*
Western hemlock	0	-	2	0.1	-	-
Totals	288	100.0	1,423	100.0		

[a]Excludes gravel bars, driftwood, fence-posts, and trees >50 m from the river.

[b]Ratio of utilization to availability; ratios larger than 1 with significant X^2 values indicate a preference for a perch type and ratios smaller than 1 with significant X^2 values indicate an avoidance of a perch type.

[c]Various species.

*$P < 0.001$.

ern Washington has also been documented on the Nooksack River (Stalmaster and Newman 1979) and Skykomish River (Hansen and Bartelme 1980).

Of 94 measured trees at 9 roosts, black cottonwood was most commonly used (53%) by eagles, followed by Douglas-fir (40%) and western red cedar (6%). Eagles roosting along the Nisqually River or its side-channels used cottonwoods almost exclusively, and eagles roosting off the river used firs and cedars. The 94 roost trees were a mean of 49 m in height (29-76 m range) and 101 cm in diameter (43-180 cm range). Thirteen of 94 roost trees (14%) were dead, having died from either inundation or girdling by beavers (*Castor canadensis*).

Cottonwood, fir, and cedar are the most common roost tree species used by eagles on the Skagit, Nooksack, and Skykomish rivers (Hansen et al. 1980, Anthony et al. 1982), similar to our findings. Heights and diameters of roost trees in our study area generally were larger than trees in 13 communal roosts measured throughout the Pacific Northwest (Anthony et al. 1982). Mean diameters of trees in 8 of the 9 communal roosts surpassed the 81-cm diameter minimum specification for old-growth (Anthony et al. 1982). Only fir trees in the Bluff roost were not old-growth; they were being managed for harvest prior to roost discovery. Fir trees in the Muck Creek roost were exceptionally tall, up to 76 m in height, and dead cedar trees in the Cabin Creek roost were exceptionally wide, up to 180 cm in diameter.

Protective Management

Wintering populations of bald eagles need an abundant, accessible, and uncontaminated food source; old or mature forests for perching and roosting; and seclusion from disturbing human activities (Steenhof and Brown 1978). These elements exist in the study area despite the close proximity of the FLR and the NIR to large metropolitan centers and associated human influences. However, management is needed to enhance conditions to provide for both the existing and an expanding eagle population. We recommend enhancing existing chum salmon spawning habitat and restoring degraded sites, especially in areas secluded from human activity, as well as allowing higher spawning escapements for the drainage (reducing commercial and sport harvest). Old-growth and mature forests along the Nisqually River and Muck Creek need to be continually protected from harvest, as is the present FLR policy. Riparian forest management on the NIR also should consider habitat needs of bald eagles. Disturbing human activity should be selectively restricted

during the winter season. This includes regulating (or monitoring) boating and helicopter traffic along the Nisqually River, and eliminating explosive ordnance disposals and other disturbing military firing activity near Muck Creek (Stalmaster 1994).

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A Comparison of Whole and Thin-Sectioned Otolith Aging Techniques and Validation of Annuli for Arctic Grayling

Abstract

Information on age and growth is essential for the conservation and management of fish species. Age is often estimated using the banding structure in otoliths, but the technique used can influence the estimate, especially in slow-growing, long-lived species. Counts of translucent bands from both whole and thin-sectioned Arctic grayling (*Thymallus arcticus*) otoliths from the Kuparuk River, Alaska, gave similar age estimates. Age estimates from whole otoliths were less variable, particularly for older age groups, and were much easier to prepare and read than thin-sections. Comparison of growth of individual tagged fish to a von Bertalanffy growth model revealed that the translucent rings are true annuli. This approach to validation may be most useful in northern latitudes where other techniques are impractical. Our study shows that whole otoliths provide a fast, reliable, cost-effective technique for age estimation of this long-lived, slow-growing fish species common to the North American Arctic.

Introduction

Arctic grayling, *Thymallus arcticus* (Pallus), are widely distributed in the Arctic, often dominating fish communities in streams and lakes (Tack 1971, Carl et al. 1992). They are slow-growing, long-lived, and late-maturing, especially in the northernmost populations (Reed 1964, Beauchamp 1982, Northcote 1995). Information about age at maturity, longevity, and length-at-age is essential for the management and conservation of the species.

Age of fishes is typically estimated by counting bands in such hard parts as scales, fin rays, and sagittal otoliths, but both the hard part examined and the aging method used can yield different age estimates. Otoliths are considered the most accurate bony structures for estimating ages of slow-growing, long-lived species because they are less susceptible to resorbtion compared to more metabolically active parts (Beamish and McFarlane 1983). Lateral views of whole Arctic grayling otoliths yielded band counts which were more closely correlated with fish size than were band counts from scales, fin rays, whole and sectioned vertebrae, and whole and sectioned opercula (Yole 1975, Sikstrom 1983, Merritt and Fleming 1991). Cross-sections of otoliths have been advocated for long-lived, slow-growing species because differentiating closely spaced bands near the outside edge of an otolith can be difficult using whole otoliths. This occurs most often when the annual growth increment is small and fish have large otoliths (as is typical of older fish) and leads to an underestimate of the true age of the fish. For example, Power (1978) found that lateral views of whole otoliths yielded underestimates of age of Arctic whitefish (*Coregonus clupeaformis*) by up to 20 years when compared to otoliths cross-sectioned using the 'broken and burned' method. Barber and McFarlane (1987) and Kristoffersen and Klemetsen (1991) found that broken and burned otolith sections gave higher ages than surface-examined whole otoliths for some stocks of Arctic char (*Salvelinus alpinus*). Thin sections, in which a cross-section is sliced from the otolith and examined microscopically, have given higher estimates of ages than have whole otoliths or broken and burned sections for some species (Casselman 1983). Merritt and Fleming (1991) found that whole otoliths of Arctic grayling produced higher estimates of age than did broken and burned otoliths, but they did not examine thin-sectioned otoliths.

An additional problem in estimating the age of fish using hard parts is knowing the frequency of formation of the bands. Translucent bands on otoliths of Arctic grayling are assumed to represent annuli (Sikstrom 1983), but this assumption has not been tested because many of the validation methods are impractical at extreme northern

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latitudes. One approach that has been used in some species where other approaches cannot be used is to develop a von Bertalanffy growth model assuming the translucent bands are annuli and to determine if the model produces growth parameters (e. g., mean asymptotic length, L_∞) that are realistic (Casselman 1987, DeVries and Frie 1996, Burnham-Curtis and Bronte 1996). This method can indicate the reasonableness of the annuli assumption, although it is not definitive. The best technique for estimating the age of a fish is one in which the frequency of formation of the banding structure in the hard part has been validated.

Our objectives in this study were to: 1) compare age estimates for Arctic grayling using polished whole otoliths and otolith thin-sections, and 2) validate formation of otolith annuli by coupling the von Bertalanffy growth model with growth of individual tagged fish. We provide an alternate approach to validating annuli formation which may be useful in high latitudes where other techniques are impractical.

Methods

Fish Collection

Arctic grayling were collected from a reach of the upper Kuparuk River near where it crosses the Dalton Highway on the North Slope of Alaska (68°N, 149°W; Figure 1). As part of a long-term study of the population dynamics of Arctic grayling begun in 1985, fish have been collected, anesthetized (MS-222), weighed (±1 g), measured (±0.1 cm total length (TL)), tagged (Floy FD-68B T-bar anchor tags), and released into the Kuparuk River (Figure 1). During July-August 1986-1992 we seined, measured and froze 531 fish. Later, sex of each specimen was determined, and both sagittal otoliths were removed and stored dry in envelopes.

Aging Technique Comparison

Age estimates from whole and thin-sections should differ most in larger, older fish (Casselman 1987); therefore, sub-adult and adult fish 21.5 to 43.6 cm TL (26 males, 20 females) were used to compare techniques. One otolith from each fish was read whole and the other was thin-sectioned. The distal surface of each whole otolith was polished for 3 to 5 sec using 400-grade wet-dry sandpaper and a drop of clove oil which made the translucent bands more distinct (DeVries and Frie 1996). Thin-sections (about 0.18 mm thick) were made by embedding unpolished, whole otoliths in black wax on a cardboard backing and cutting them transversely through the sulcus acusticus on the dorsal-ventral axis with a diamond saw (Secor et al. 1992, Almeida and Sheehan 1997). Exploratory work revealed that this section (Figure 2a) had the most distinct translucent bands.

Opaque and translucent band pairs in each of two preparations were counted twice on separate occasions by two readers. Readers had no knowledge of their previous readings, the other reader's results, or the total length of the fish. Polished whole and thin-sectioned otoliths were placed on a black background (proximal-side down for whole otoliths) and wetted with liquid dish soap or a 50/50 glycerin/water solution to enhance the translucent bands. The otoliths were then observed through a microscope at magnifications of 10X to 50X with reflected light. Neither reader had previous experience reading otoliths, so they were trained at the National Marine Fisheries Service Age and Growth Lab (Woods Hole, MA) at the start of this project.

Age was estimated by assuming that each opaque and translucent band pair represented one year; the opaque bands result from fast, summer growth and translucent bands from slow, winter growth (Sikstrom 1983, Jearld 1983, Secor et al. 1992). A translucent band that generally followed the overall shape of the otolith was considered to be an annulus. If a translucent band appeared faint, very narrow, ephemeral and discontinuous, it was considered a "check," meaning a false annulus that was not counted (Figure 2b). An incomplete opaque band at the edge of an otolith was assigned a "+," which represented incomplete summer growth. Readings of polished whole otoliths were generally done on the dorsal and ventral lobes (Figure 2b), where translucent bands were usually easiest to identify. For the thin-sections, counts were done along the sulcus, where the translucent bands were best-defined (Figure 2b). Thin-sections were often turned over and counted on the other side, particularly when the thin-sections had relatively large numbers of annuli.

Repeated measures ANOVA was used to determine if there was any significant difference in age between readers or techniques. The age esti-

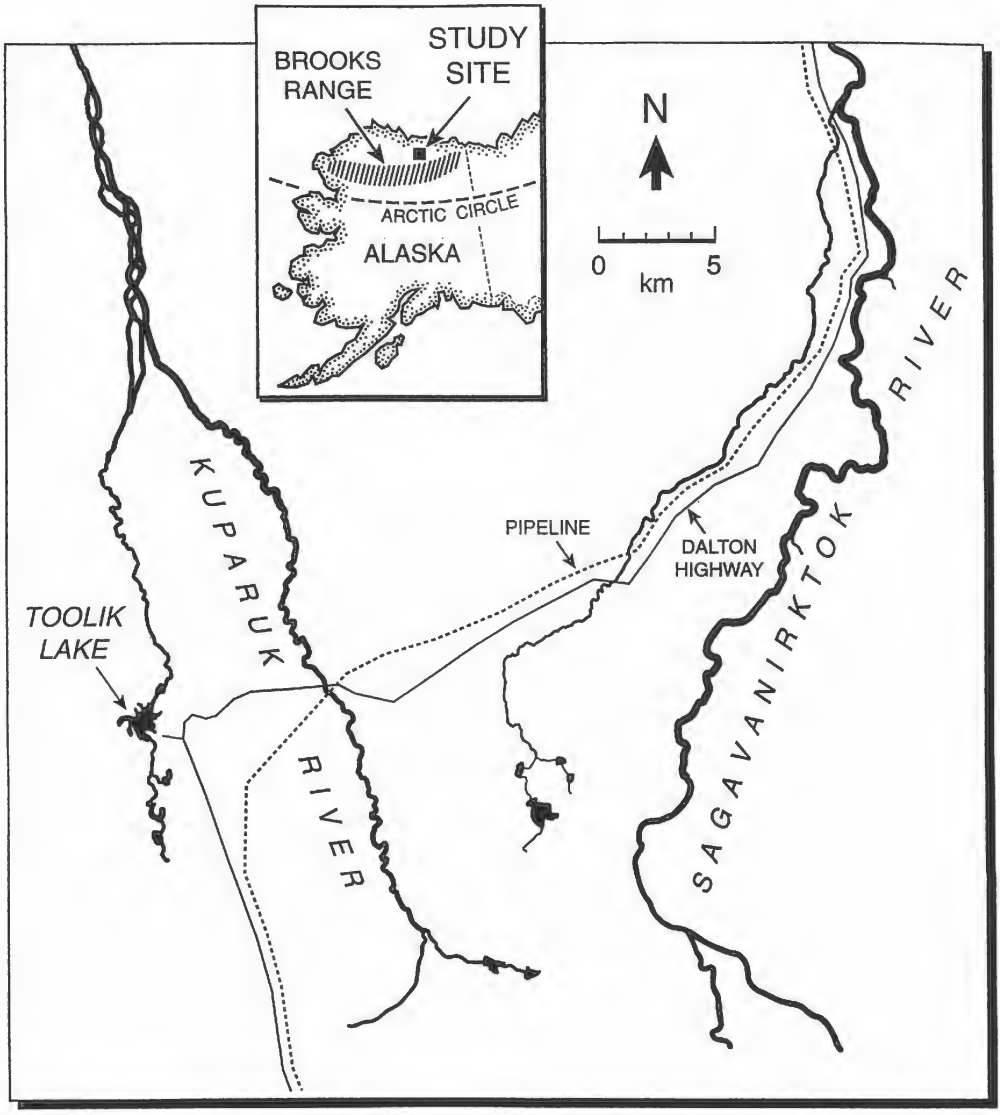

Figure 1. Map of the study area in the upper Kuparuk River watershed. Fish were captured near where the haul road crosses the Kuparuk River.

mate (by method) was the repeated measure and reader the main effect (Statview 4.5, Abacus Concepts 1992). To examine the variability in age estimate by method, we plotted standard deviation against age and used a t-test to determine if standard deviations differed between methods. The mean and standard deviation from four readings (two readers, two reads per method) were computed for each otolith for each method.

Validation

A von Bertalanffy growth model was fitted to length-at-age data with the equation: $L_t = L\infty\ (1-e^{-k(t-t_0)})$ where L_t is the total length (cm) at age

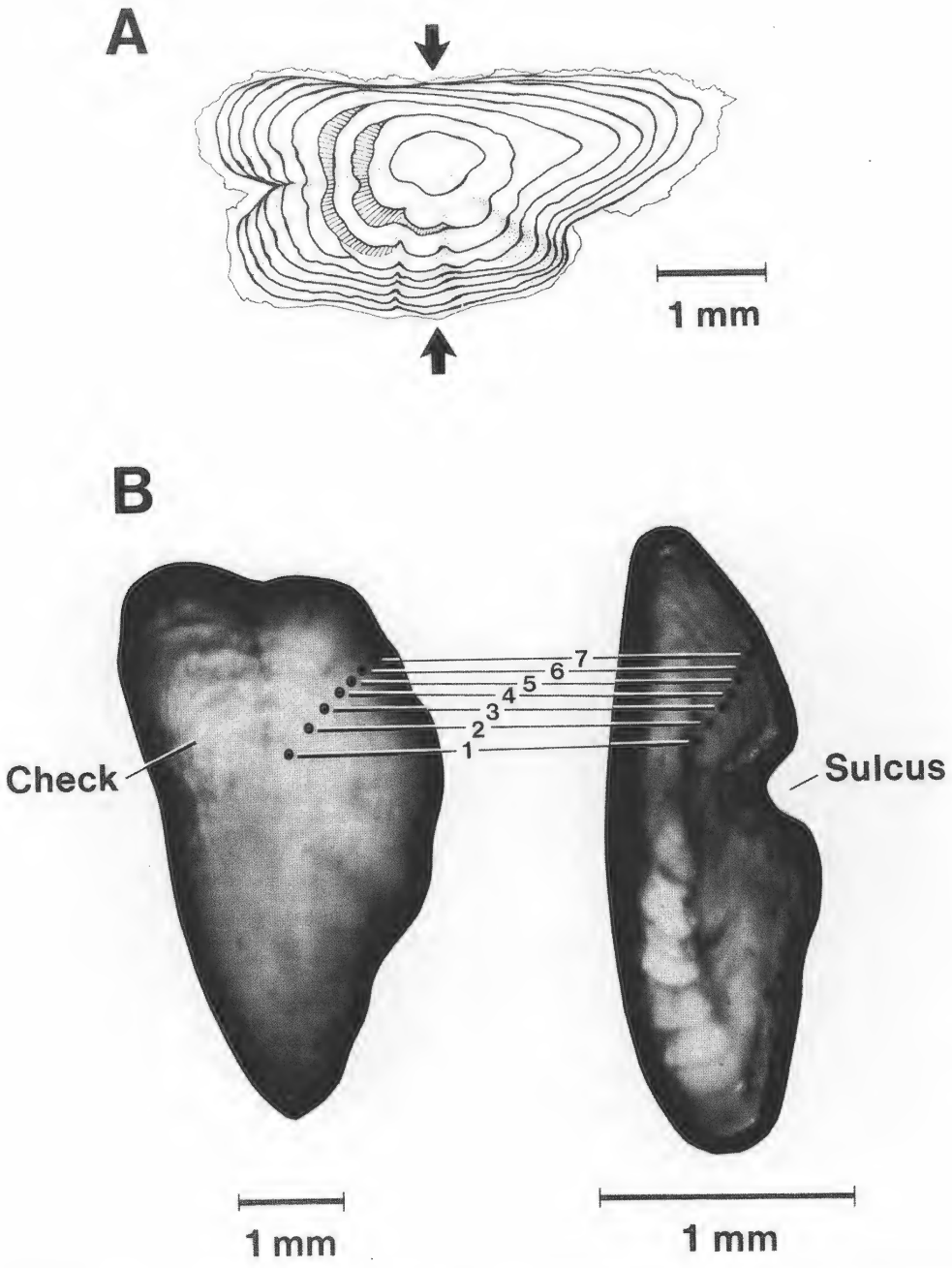

Figure 2. a) Diagram of an Arctic grayling otolith. The arrows indicate the cross section used for thin-sectioning otoliths in this study. b) Photographs of the lateral surface of a polished whole otolith (left) and corresponding thin-section (right) taken from an age-7 Arctic grayling, with dots indicating annuli. Size scales are different in the two photographs.

t (years), $L\infty$ is the asymptotic total length, k is the growth coefficient, and t_0 is the hypothetical age of otolith formation using a nonlinear curve fitting package (SAS 1985). In developing this model, we assumed that translucent bands were formed annually. Polished whole otoliths were used to estimate the age of 193 males, 166 females and 76 immature fish (≤ 25 cm TL). Immature fish were used in both male (n = 269) and female (n = 242) growth curves.

We assessed the validity of assuming that translucent bands are annuli by comparing length data from tagged and recaptured fish to the predictions of the von Bertalanffy growth model. Data from tagged fish were of two types: 1) adult fish that had been caught at least twice and were killed to determine their age-at-final-capture and backcalculated age-at-previous-capture, and 2) juvenile fish that had been tagged at a small size where initial age could be well-estimated and were later recaptured several times. Fish used for the validation were not used to develop the von Bertalanffy growth model. A total of 50 adult fish (22 females and 28 males) were used to determine the age-at-final-capture (based on whole otoliths). Age-at-previous-capture was backcalculated by subtracting the number of years between previous capture and final capture from the age-at-final-capture. A total of 11 females and 24 males were tagged as juveniles and recaptured over a period of 7 years. Initial age was estimated using whole otoliths from fish of the same size from the same year-class and subsequent ages estimated by adding years-at-large since initial capture. The length data for both age-at-final-capture and the age-at-previous-capture were then compared to the length-at-age predictions of the von Bertalanffy growth model using the 95% confidence limits of predicted lengths (Draper and Smith 1981). If the translucent bands are annuli, we expect less than 5% of the length-at-age data from the tagged fish to lie outside the 95% confidence limits.

Results

Technique Comparison

Whole and thin-sectioned otoliths gave the same age estimates, but age estimates from thin-sections were more variable than those from whole otoliths. We found no difference in the estimated age of a fish by method or by reader, indicating that both methods gave similar age estimates (Table 1). We also found no difference in age estimates by technique between males and females ($F= 0.52$, $p=0.66$). Age estimates from thin-sections were more variable at every age, and variation increased more rapidly with age for thin-sections than for whole otoliths (Figure 3). The mean standard

TABLE 1. Results of a repeated measures ANOVA relating estimated age to reader (first or second) and technique (thin-sectioned or whole) otoliths factors.

Source	df	Mean Square	F-value	p-value
Reader	1	38.5	0.722	0.39
Subject (Group)	92	53.39		
Measurement Technique	3	0.037	0.031	0.99
Technique Reader	3	1.48	1.25	0.28
Technique Subject (Group)	276	0.99		

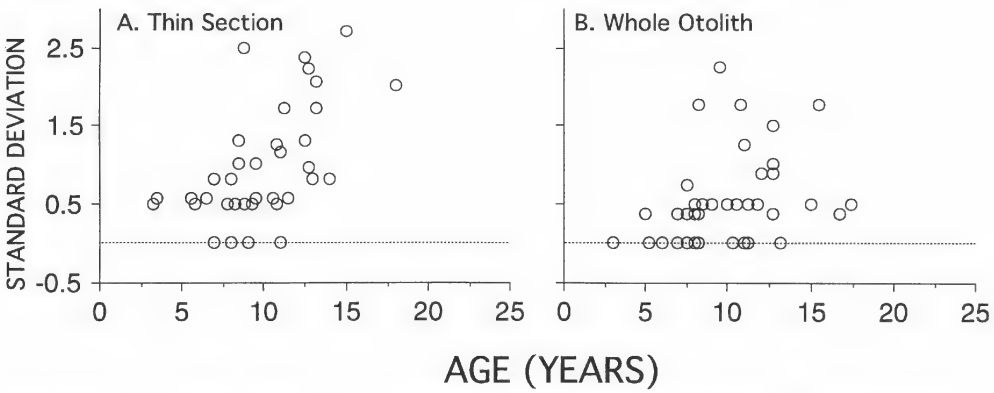

Figure 3. Relationship between standard deviation and age for thin-section (n = 46) and whole otolith (n = 46) techniques.

deviation for thin-sectioned otoliths age estimates (0.92) was significantly higher (n=46, t=3.11, $p<0.001$) than the mean standard deviation for whole otolith age estimates (0.51). The higher variation in thin-section age estimates resulted from difficulty interpreting the banding structure, not from differences between readers. Thin-sections had faint rings, especially near the outer edges, confusing discontinuities, and the first annulus was often difficult to discern. Readers felt interpreting rings on the thin-sections required more judgment decisions than did interpreting rings on whole otoliths.

Annuli Validation

The von Bertalanffy growth model exhibited the classic asymptote at older ages, and estimates of L_∞ were similar to the largest fish measured for both sexes. Fish were 5 to 43.6 cm TL and from 0 to 22 years old. The largest female was 40.7 cm TL and 11 years of age, while the oldest female (22 years) was only 36 cm TL. The largest male was 43.6 cm TL and 11 years old, while the oldest male (22 years) was 42.6 cm TL. The parameters ($\pm$ 95 % confidence limits) of the von Bertalanffy growth model equations were: female - $L_\infty = 37.9$ (37.2 - 38.4), $k = 0.27$ (0.26 - 0.28), $t_0 = -0.4$ (-0.5 - -0.2), $r^2 = 0.96$; male - $L_\infty = 41.6$ (40.9 - 42.4), $k = 0.22$ (0.21 - 0.23), $t_0 = -0.5$ (-0.7 - -0.3), $r^2 = 0.98$. The growth equations indicate that males ($L_\infty = 41.6$ cm) reach a larger maximum size than do females ($L_\infty = 37.9$) but grow more slowly (Figure 4a & b).

Only 2.6% of the 187 observations of length-at-age from tagged fish were outside the 95% confidence interval for the predicted length-at-age (Figure 4). Adult fish used for otolith age estimates were typical of fish from the Kuparuk River (females: ave. 34.7 cm TL, range 27.5 to 37.1 cm TL; males: ave. 36.6 cm TL, range 27.5 to 39.8 cm TL). These fish were approximately 8 - 9 years old; the oldest fish was 13 years old and the youngest backcalculated age was 6 years. Time between previous capture and final capture of tagged fish ranged from 1 to 5 years; 24 fish were recaptured after 1 year, 16 after 2 years, 8 after 3 years, 1 after 4 years and 1 after 5 years. For females, no length-at-final-capture and only 1 length-at-previous-capture fell outside the 95% confidence interval (Figure 4a). One observation is less than the 2.2 observations (5% of 44 observations) expected to lie outside the 95% confidence limit. For males, no length-at-final-capture and 2 length-at-previous-captures fell outside the 95% confidence interval (Figure 4b). Approximately 3 observations are expected to lie outside the 95% confidence limits (2.8; 5% of 56). In all cases, the length-at-age estimates for both final-capture and previous-capture were well within the range of the data used to construct the von Bertalanffy growth model.

The length-at-age and the growth pattern of fish tagged as juveniles also closely followed the von Bertalanffy growth model (Figure 4e & f). For both males and females, the average initial size at tagging was 24 cm TL with an estimated age of 4 years. Fish were at large for between 3 and 7 years between initial and final capture and were recaptured 3 to 6 times. Final size ranged from 33 to 40 cm TL and final age ranged from 6 - 12 years. Of the 38 estimates of length-at-age for females and 49 estimates for males, only two length-at-age observations (one male, one female) lie outside the 95% confidence interval. Overall, growth curves for individual fish lie within the 95% confidence interval, although one or two individuals apparently grew much faster at younger ages than expected based on the von Bertalanffy growth model.

Discussion

Cross-sections (broken and burned or thin-sections) of otoliths, rather than whole otoliths, have been advocated for aging long-lived, slow-growing fishes (Power 1978; Beamish 1979a, 1979b; Barber and McFarlane 1987; Kristoffersen and Klemetsen 1991). Worthington et al. (1995), however, suggested using aging methods that are uncomplicated and cost-effective, so long as the methods provide reliable data. Our study, like those of Baker and Timmons (1991) and Burnham-Curtis and Bronte (1996), demonstrates that for some species whole otoliths need only be polished to produce age estimates similar to and more precise than estimates derived from cross-sections even in a long-lived, slow growing species. Thin-sectioning did not yield different ages nor did it improve the precision of age estimates compared to those from whole otoliths. Thin-sections had very faint rings, especially near the outer edges, a sometimes indistinguishable first annulus, and confusing discontinuities. In addition, they were time-consuming to prepare, fragile and difficult to store. Similar difficulties were reported for

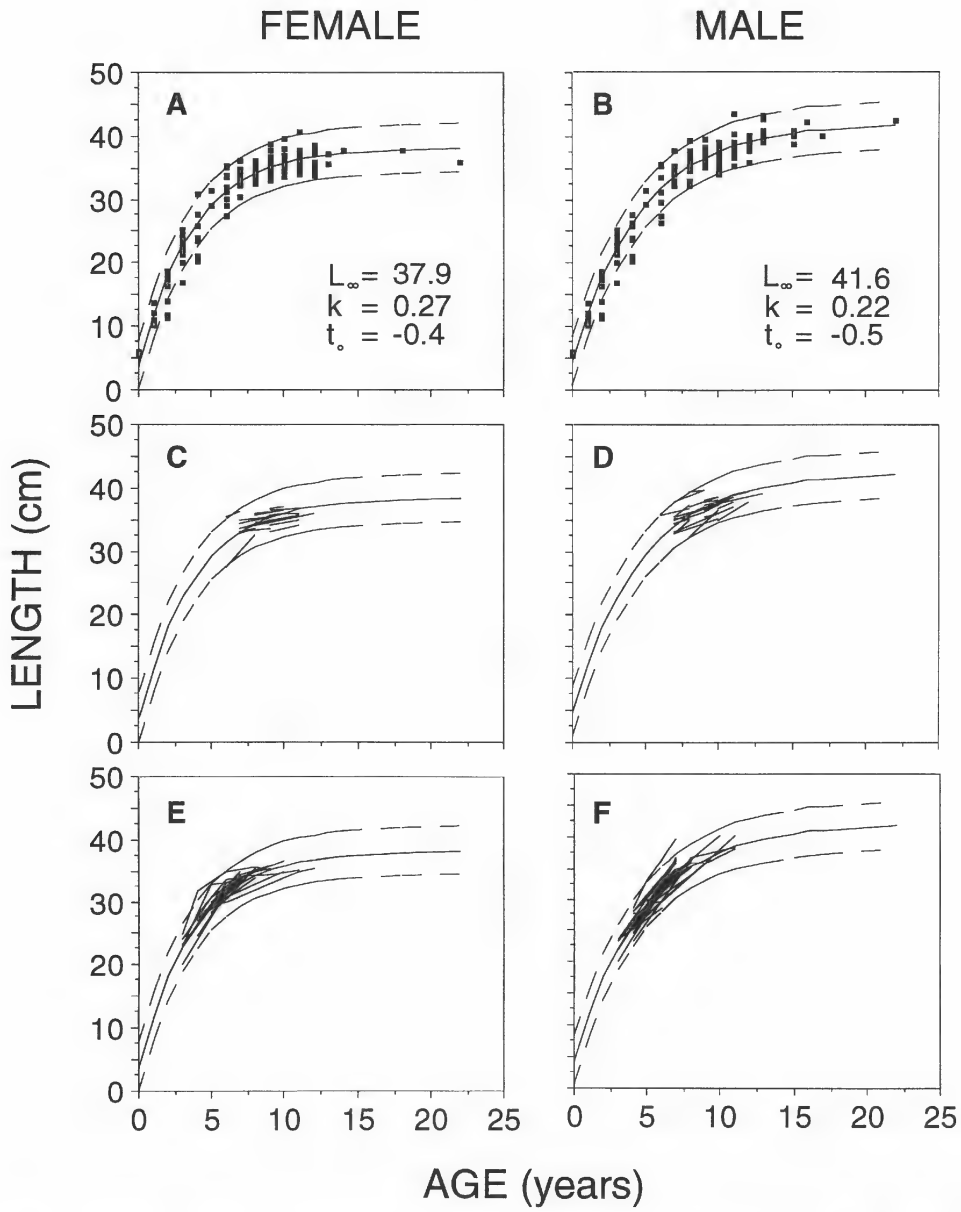

Figure 4. von Bertalanffy growth model compared to length-at-age data. A and B) Length-at-age data for Kuparuk River Arctic grayling used to parameterize the von Bertalanffy growth model (A: female, n = 242; B: male, n = 269). C and D) Age-at-length-at-final recapture and length-at-age-at-previous capture of tagged adult fish (C: female, n = 22; D: male, n = 28). E and F) Length-at-age-at-recapture for fish tagged as juveniles. (E: female, n = 11; F: male, n = 24). The curved solid line in each panel is the mean prediction of the von Bertalanffy growth model; curved dotted lines are the upper and lower bounds of the 95% confidence interval for a predicted length. Symbols in panels A and B indicate individual fish length and age estimates. Short straight solid lines in panels C, D, E and F connect the lengths-at-age for individual fish measured several times to indicate growth.

broken and burned Arctic grayling otoliths (Merritt and Fleming 1991). We recommend the use of whole otoliths for estimating age of Arctic grayling as they were much easier to prepare and read than thin-sections and provided the same age estimates.

The comparison between tagged fish growth and the von Bertalanffy growth model predictions indicate that the translucent bands represent annuli. The length-at-age data for virtually all (97.3%) adult and juvenile fish lie within the 95% confidence interval, and the pattern of individual fish growth over time is consistent with the von Bertalanffy growth model. The strongest evidence is the conformation of size-at-age of the juvenile fishes to the model because these fish are rapidly growing and the confidence limits are narrow. Adult grayling growth is asymptotic as predicted, but confidence limits in this region of the growth curve are large. This analysis allowed us to follow the growth of individual fish from 4 years old until they were 12 years old. We followed them through the rapid growth phase and into the asymptotic growth phase where detection of annuli becomes problematic. By coupling juvenile growth with an analysis of adult growth we were able to validate formation of annuli over the age range of 3 to 13 years. Determining the timing and frequency of otolith increment formation using known age fish and marking otoliths is the most definitive method of validation (Geffen 1992, DeVries and Frie 1996), but the application of chemicals to mark otoliths in wild fish populations is currently restricted by the United States Food and Drug Administration. Until this kind of information is available for Arctic grayling, our analysis indicates that the assumption of annular formation of translucent bands in Arctic grayling otoliths is reasonable.

Testing the von Bertalanffy growth model based on the assumption of annual ring formation and using tagged fish provides an alternative method for validating otoliths in fish populations at high latitudes and remote areas where other methods are not feasible. Incremental edge analysis, in which fish are captured year-round to analyze the development of translucent and opaque bands on otoliths (Beamish and McFarlane 1983), is not possible because Arctic waters are often inaccessible from November to May. Analysis of the changes in length-frequency distributions over time (McNew and Summerfelt 1978, Weatherley and Gill 1987) does not work well because as the year-classes age, the length distribution of individual cohorts overlap and become indistinct. Identifying individual age cohorts becomes impossible for older fish. Gauldie (1990) suggested that in some temperate and tropical fish species, weight varies widely within a year and the banding structure of otoliths may be linked to gains in weight rather than length. This might limit the usefulness of the von Bertalanffy growth model based on length as a validation method in some fish populations. In Arctic grayling, as in many northern latitude species (e.g., Fechhelm et al. 1995), growth in length and weight show a strong positive correlation ($r^2 = 0.96$), and their rapid growth in the summer (up to 80 g and 1.5 cm TL) followed by no growth over winter is ideal for the production of distinct annual bands on otoliths (Jearld 1983, Secor et al. 1992, Deegan and Peterson 1992). Thus, northern fish have ideal growth characteristics for using the von Bertalanffy growth model linked to tagged fish growth to validate the banding structure of otoliths.

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Evaluating the WATBAL Sediment Loading Model, Clearwater National Forest, Idaho

Abstract

Efforts to protect water quality while managing national forests for logging purposes are currently constrained by limited information on the application, interpretation, and validation of sediment loading models. For years, these models have been used to predict the impacts of logging, road-building, and fires on sediment loading to streams. However, in the Clearwater National Forest, where the WATBAL sediment loading model is used, model results have never been compared to actual field measurements. Without model validation, forest managers are working with unverified information regarding the impacts of logging activities on aquatic systems. To effectively manage our national forests and their aquatic ecosystems, we must provide accurate information to forest managers. This paper presents the results of comparing the WATBAL output to field measurements of sediment loading to streams in the Clearwater National Forest, ID.

Introduction

In the northern Rocky Mountains, national forests are managed for two primary purposes which are often at odds with each other: logging and recreation. Logging and associated roadbuilding activities negatively impact both water quality and aquatic ecosystems by increasing sediment loading in the streams (Megahan and Kidd, 1972; Megahan, 1975; Meehan, 1991; Ketcheson, 1986). Unfortunately, most quantitative methods for evaluating sedimentation are limited by a poor understanding of the processes involved (Klemes, 1986). Thus, attempts to predict sedimentation have focused upon land-use based models (Gloss, 1995).

Due to the complexity of sediment yield modeling, efforts within the United States Forest Service (USFS) have been "based primarily on professional judgment of field hydrologists with some extrapolation of published research" (Knighton and Solomon, 1989, p. 345). The "Guide for Predicting Sediment Yields from Forested Watersheds" (Cline, et. al, 1981) was developed by the Northern and Intermountain Regions of the USFS to provide a consistent framework under which the individual national forests would develop their own sediment yield models. In the Clearwater National Forest, the USFS uses the sediment loading model WATBAL (Patten, 1989) to predict the impacts of logging and logging-related road building. The output is given in two components: mass wasting and surface erosion.

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The objective of this study is to evaluate the WATBAL model as a tool for predicting the cumulative effects of land management activities on sediment yield in the Clearwater National Forest, ID. The intent is to provide information necessary to more successfully apply and interpret the WATBAL model for management of non-point source sediment caused by logging and recreation. Specific objectives of the study are to:

1) Determine if average annual sediment yields predicted by WATBAL are comparable to average annual sediment yields computed from field data.

2) Test the relations between stream discharge, precipitation, and the accuracy of WATBAL predictions.

To accomplish these objectives, the measured and modeled sediment yield values were compared to field measurements of suspended and bedload sediments in two watersheds. In addition, the errors (model minus measured sediment loads) were compared to stream discharge and precipitation to determine whether or not the magnitudes of the errors are a function of discharge or precipitation. In addition, the WATBAL model was examined for other potential sources of error, particularly those associated with roads or the scale of analysis (minimum mapping unit).

Study Site and Watershed History

This study evaluates two watersheds in north-central Idaho; the upper Lolo Creek and Pete King

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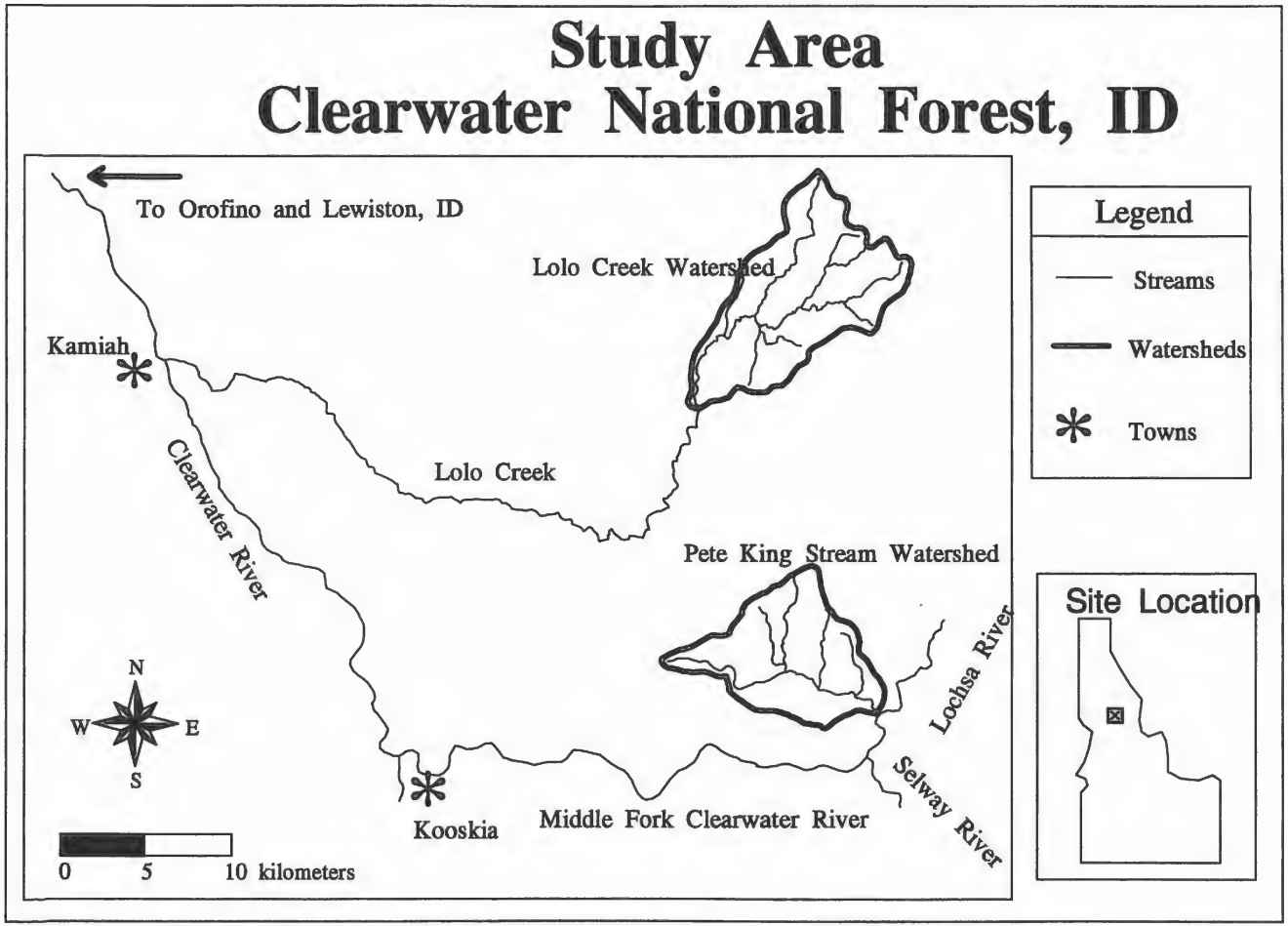

Figure 1. Study site location map.

TABLE 1. Basic watershed characteristics (from WATBAL output files).

	Lolo Creek	Pet King King Stream
Elevation (meters)	902-1845	450-1591
Total Area (sq. kilometers)	103	72
Av. Annual Precipitation (cm.)	122	97
Avg. Annual Runoff (cm.)	61	41

Stream watersheds (Figure 1, Table 1). These were selected because they are the two watersheds with the longest sampling histories (9 and 19 years, respectively) in the Clearwater National Forest. The hydrology is dominated by spring snowmelt, with approximately two-thirds of the annual precipitation occurring between November and April. The geology is predominantly Belt Supergroup (gneiss and schist) and Idaho Batholith granites. Landuses are primarily logging and recreation.

Information regarding the Lolo watershed indicates that logging and roadbuilding activities have occurred almost continuously during the years 1954 through 1991. By 1991, the last year that logging occurred in the Lolo Creek watershed, 4708 hectares (11,634 acres) (46.4% of the watershed) had been disturbed. Table 2 describes predicted and measured sediment loads and stream discharge for Lolo Creek. Field measurements of sediment yields have been collected only since 1984.

Landforms within the Pete King Watershed consist of approximately 50% breaklands and 50% rolling uplands and mountains. The breaklands typically have very high mass wasting and sediment delivery potential (Jones, 1992). Human activities in the watershed began in 1953 with the introduction of the first logging road. Logging, fire, and roadbuilding activities have continued through 1991. A complete history of mass wasting events has not been developed. However, a number of landslides occurred in the 1970's, dumping excessive amounts of sediment into Pete King Stream (Jones, 1992). A 1978 event, and another in 1987, are obvious when viewing sediment loading data (Table 3). Both events were caused by road failures (D. Jones, pers. comm, 1995). To date, 2582 hectares (6,381 acres) of forest have been harvested and 256 kilometers (153.6 miles) of roads have been constructed, covering 36.3% of the watershed. In 1934, a large fire burned 34% of the watershed—thus, in the last 60 years, approximately 70% of the watershed has been disturbed (Jones, 1992). Table 3 describes predicted and measured sediment loads and stream discharge for Pete King Stream. Field measurements of sediment yields have been collected only since 1976.

Model Description

The WATBAL sediment loading model is derived from the "Guide for Predicting Sediment Yields from Forested Watersheds" (Cline et al., 1981). This manual sets the objectives, standards, limitations, assumptions, and conceptual background for all sediment yield models in the Northern and Intermountain Regions of the USFS. The two

TABLE 2. Original data, Lolo Stream.

Dates	Mean Discharge	Maximum Discharge	Field Meas. tons/sq. mi./yr.	WATBAL tons/sq. mi./yr.	WATBAL.- Field meas.
10/1/84—9/30/85	89.5	312.1	20.7	9	-11.7
10/1/85—9/30/86	97.9	298.6	17.1	9	-8.1
10/1/86—9/30/87	132.2	575.9	75.6	10	-65.6
10/1/87—9/30/88	57.7	177.9	9.8	9	-0.8
10/1/88—9/30/89	81.9	326.5	28.9	8	-20.9
10/1/89—9/30/90	75.8	278	36.9	8	-28.9
10/1/90—9/30/91	90.4	231.3	39	8	-31
10/1/91—9/30/92	69.1	168.7	20.5	8	-12.5
10/1/92—9/30/93	88.4	311.2	no data	7	
10/1/93—9/30/94	52.3	187.4	26.6	7	-19.6

TABLE 3. Original data, Pete King Stream.

Dates	Mean Discharge	Maximum Discharge	Field Meas. tons/sq. mi/yr.	WATBAL tons/sq. mi./yr.	WATBAL. - Field meas.
10/1/75—9/29/76	96.6	202.6	59	56	-3
10/1/76—9/30/77	24.1	46.9	8.4	50	41.6
10/1/77—9/30/78	40	131.2	17.4	42	24.6
10/1/78—9/29/79	51.2	212.1	173.9	40	-133.9
10/1/79—9/30/80	37.7	92.7	20.3	39	18.7
10/1/80—9/30/81	45	83.5	33.1	38	4.9
10/1/81—9/30/82	72.5	163.9	70.2	36	-34.2
10/1/82—9/30/83	50	121.2	19.4	33	13.6
10/1/83—9/30/84	57.7	153.7	69.6	33	-36.6
10/1/84—9/30/85	46.6	131.7	44.6	32	-12.6
10/1/85—9/30/86	59.5	179.1	26.1	31	4.9
10/1/86—9/30/87	28.9	67.4	401.3	34	-367.3
10/1/87—9/30/88	29.1	80.9	58.7	33	-25.7
10/1/88—9/30/89	68.8	205.6	71	29	-42
10/1/89—9/30/90	29.9	59.8	54.8	29	-25.8
10/1/90—9/30/91	35.4	76.2	16.6	29	12.4
10/1/91—9/30/92	24.7	48.2	16.9	28	11.1
10/1/92—9/30/93	32	78.6	18.1	28	9.9
10/1/93—9/30/94	27.5	65.5	20.4	28	7.6

limitations/assumptions that are of particular interest to this analysis are (pgs. 3-4):

"1. Sediment yield can be usefully displayed as an expected average annual event although it is subject to considerable variability from year to year and within any single year.

2. Model outputs are primarily intended to indicate trends and to compare management alternatives and secondarily to provide quantified estimates of sediment yield."

The WATBAL model has been under constant development since 1973, with a stated objective of "estimating water yields in response to cumulative watershed development and vegetative manipulation and recovery over time" (Patten, 1989, pg. 1). At present, WATBAL "is designed to simulate the potential and most likely effects of primary forest management practices (timber harvest, road development, and fire) on the responses of watershed and water resource systems with regard to stream flow and sediment regimes." (Patten, 1989, pg. 1) In the Clearwater National Forest, the WATBAL program and associated data files serve as the primary watershed inventory (Patten, 1989).

Watersheds are divided into areas that are relatively homogeneous (landtypes), for which a number of response characteristics are determined. The physical characteristics measured include: slope angle, slope shape, slope length, surface drainage, soil depth, soil texture, soil structure, soil consistency, bedrock type, bedrock weathering, bedrock structure, and vegetative habitat. From these characteristics, each landtype is assigned a series of hazard ratings which describe potential a) rotational mass erosion, b) debris avalanche, c) surface erosion from undisturbed soil surfaces, d) surface erosion from subsurface horizons, and e) surface erosion from the substrata (Patten, 1989). The model output from these original hazard ratings serves as the estimate of natural sediment yield in tons per square mile per year. The natural sediment yield values are based upon sediment measurements from several representative

landtypes. These measurements were then extrapolated to other landtypes using an algorithm which assumed that approximately 80% of the natural sediment is derived from long-term mass erosion processes—the remainder is from surface erosion processes related to the fire history of the landtype (Patten, 1989). Each individual landtype file also includes the stream density within that particular landtype.

Additional surface erosion is assumed to be induced, and mass erosion accelerated, by different logging, fire, and roadbuilding activities. Thus, excess (above natural amounts) erosion is a function of the type and location of different management activities. The acceleration factors for mass erosion were derived from a landslide study by Megehan, et. al (1978). Acceleration factors for roads and burned areas are also included. Surface erosion, which is assumed to be insignificant in undisturbed forests (Cline, et al., 1981), is estimated for roads, burned regions, and logged areas. Each is modified by the physical characteristics of the land and the age, size, and intensity of the disturbance.

To estimate water yields to streams, WATBAL uses a hydrograph generated from a combination of average annual discharge (a function of the average annual precipitation within the watershed) and the hydrograph of a stream deemed similar to the stream in question (Patten, 1989) (Figure 2). The average annual discharge contributes the annual volume of water and the representative hydrograph defines the shape of the hydrograph. The annual precipitation data were derived for each watershed from 1960's precipitation isohyets developed from a network of long-term storage gauges around the forest, a few recording sites west of the forest, the Natural Resources Conservation Service snow courses and climatic telemetry sites (SNOWTEL), and several stream gauges (Patten, 1989; Gayle Howard, Hydrologic Technician USFS, personal comm., 1997). Average annual precipitation and discharge are stored as constants within the watershed files, not as variables associated with landtype files.

Combining a sediment routing equation with the landtype, management, and precipitation data then allows the calculation of predicted sediment yields within a watershed (Figure 2). The WATBAL equation which calculates the total sediment yield only considers the area of the watershed. Details of stream routing, hydrology, and dynamics are not included; however, they are recognized as a weakness in the WATBAL model (Patten, 1989).

Research Methodology

Data collected by the USFS includes physical descriptions of the two watersheds, WATBAL output (sediment and mass loading), and field measurements of suspended sediment, bedload, and stream discharge. As WATBAL output is given as a yearly value, the field measurements had to be aggregated from monthly to yearly data. In addition, the suspended sediment and bedload components of sediment loading were combined to provide a single yearly estimate of total sediment loading. Stream discharge was aggregated to average and maximum monthly discharge.

There were no field components to this research, so accuracy estimates of sampling methods are not included in this analysis. Therefore, model validation focuses on a statistical comparison between measured and modeled values (Mayer and Butler, 1993; Donigian, 1981). In this analysis, subjective assessment, deviance measures (mean absolute error and the mean absolute percent error), and statistical tests (descriptive statistics, regression, and modeling efficiency) were used to evaluate the WATBAL output.

The interpretation of the Lolo Creek data was relatively straightforward; however, at Pete King Stream, there are two outliers in the dataset caused by road failures (1978 and 1987) which dumped excessive amounts of sediment into the stream. Thus, two different analyses were run for the Pete King watershed: one which included all the data, the other which represents years in which there were no catastrophic road failures.

Results

Tables 4 through 6 contain the measured and calculated sediment yields and the differences between the two. The output from the statistical comparisons of the measured and calculated sediment yields are shown in Table 7. The deviance measures are based upon the differences between the measured and calculated data and show the average absolute difference between model and measured data (MAE) and the average absolute percent error (MA%E). In the case of the MA%E,

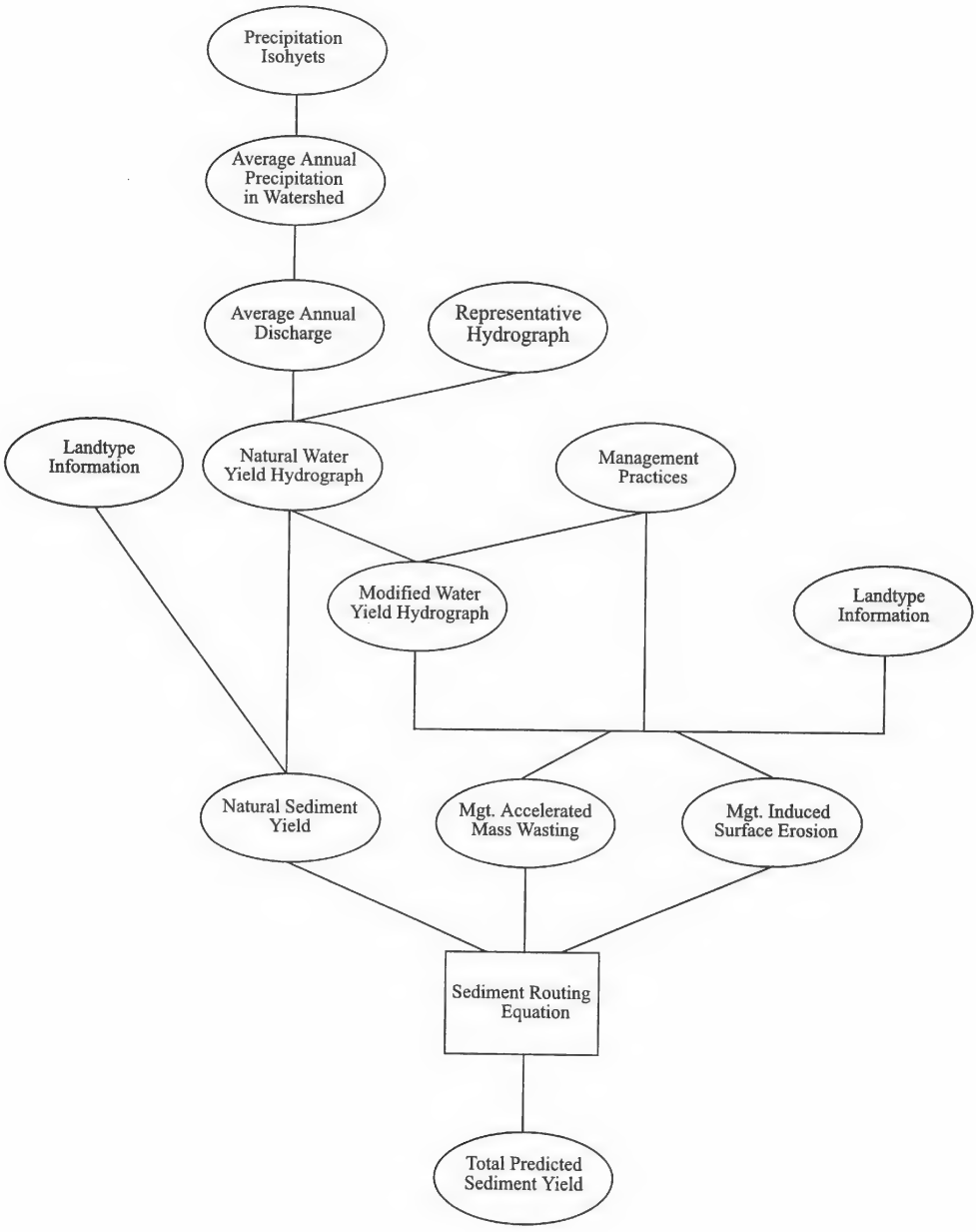

Figure 2. Generalized diagram of WATBAL model components with emphasis on precipitation data.

TABLE 4. Descriptive statistics for Lolo Stream.

	Field Meas. tons/sq. mi./yr.	WATBAL tons/sq. mi./yr.	(WATBAL)-(field meas.)
Sample Size	9	9	9
Minimum	9.8	7	-65.6
Maximum	75.6	10	-0.8
Mean	30.6	8.4	-22.1
Median	8.0	8.0	-19.6
Standard Deviance	19.26	0.9	19.0
Variance	371.1	0.8	359.4
Std. Error	6.4	0.3	6.3

TABLE 5. Descriptive statistics for Pete King Stream; data for two years with exceptionally high sediment loading excluded.

	Field Meas. tons/sq. mi/yr.	WATBAL tons/sq. mi/yr.	(WATBAL)-(field meas.)
Sample Size	17	17	17
Minimum	8.4	28	-42.0
Maximum	74.0	56	41.6
Mean	36.7	34.9	-1.8
Median	26.1	33.0	4.9
Standard Deviance	22.4	8.0	23.8
Variance	501.7	64.6	566.4
Std. Error	5.4	1.9	5.77

TABLE 6. Descriptive statistics for Pete King Stream. All data are included.

	Field Meas. tons/sq. mi./yr.	WATBAL tons/sq. mi./yr.	(WATBAL)-(field meas.)
Sample Size	19	19	19
Minimum	8.4	28	-367.3
Maximum	401.3	56	41.6
Mean	63.1	35.2	-28.0
Median	33.1	33.0	4.9
Standard Deviance	90.2	7.7	90.4
Variance	8138.6	58.8	8170.7
Std. Error	20.7	1.8	20.7

10% has been suggested as an upper limit of acceptability (Kleijnen, 1987); however, this value will vary depending upon the model and its uses (Bratley, et al., 1987). In this case, values ranging from 62 to 80 percent are clearly unacceptable. The correlation results also support this evaluation—the correlation (R^2) between the measured and calculated values is less than 0.02 in all cases.

Modeling efficiency (EF) is a dimensionless statistic which directly relates model predictions to measured data (Loague and Green, 1991). EF has a lower bound of negative infinity, while a value of one indicates that the model perfectly predicts the measured values. Models which produce values less than 0 cannot be recommended (Mayer and Butler, 1993). As the EF values in this analysis are all negative, the EF interpretation supports the output from both the deviance and regression analyses.

Figure 3 illustrates the distribution of errors at Lolo Creek. In all cases, WATBAL underestimated sediment yields. The largest underestimation occurred in 1986/87—the same year in which there were catastrophic road failures in the Pete King watershed. These are probably due to an exceptionally heavy rainfall event.

The distribution of errors at Pete King Stream are shown in Figure 4. Of the nineteen years in which data were collected, WATBAL underestimated sediment loading nine times. On average, WATBAL underestimated sediment loading by 28 tons/sq. mile/year. However, if the two catastrophic years are dropped, the mean of the distribution falls to -1.8 tons/sq. mile/year.

As all of the above comparisons show little connection between the measured and predicted sediment yield values, the question becomes explaining the reasons for this. The possibilities are numerous, and include sampling errors, annual variations in precipitation (timing, intensity, amount), and model errors. However, the only data currently available are average and maximum monthly stream discharge and monthly/annual precipitation which were then compared to the errors. The errors are defined as the difference between the WATBAL output and the measured values. At Lolo Creek, there was a significant correlation between both mean and maximum stream discharge and the errors (R^2 = 0.46 and 0.60, respectively). This is not surprising, given

TABLE 7. A statistical comparison of measured and calculated sediment yields: deviance measures (Mean Absolute Error, Mean Absolute Percent Error), linear regression (R^2, slope, intercept, standard error), and modeling efficiency (EF).

Stream	n	MAE	MA%E	R^2	Slope	Intercept	Std. error	EF
Lolo	9	21.12	62.6	0.011	.0168	7.93	0.9	-1.45
Pete King	19	43.7	79.9	-0.06	.0016	35.05	7.9	-0.11
Pete King	17	19.4	79.4	-.07	-.0002	34.95	8.3	-0.14

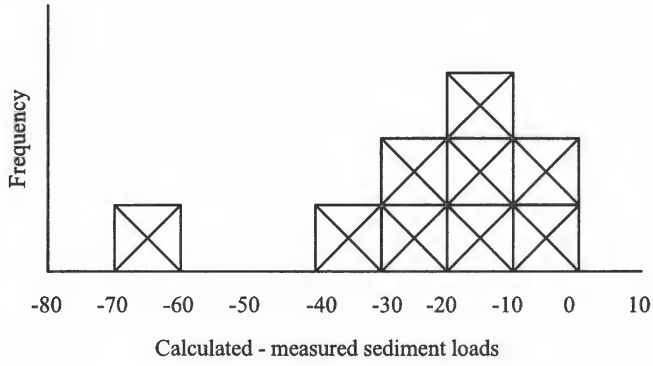

Figure 3. Distribution of errors at Lolo Creek.

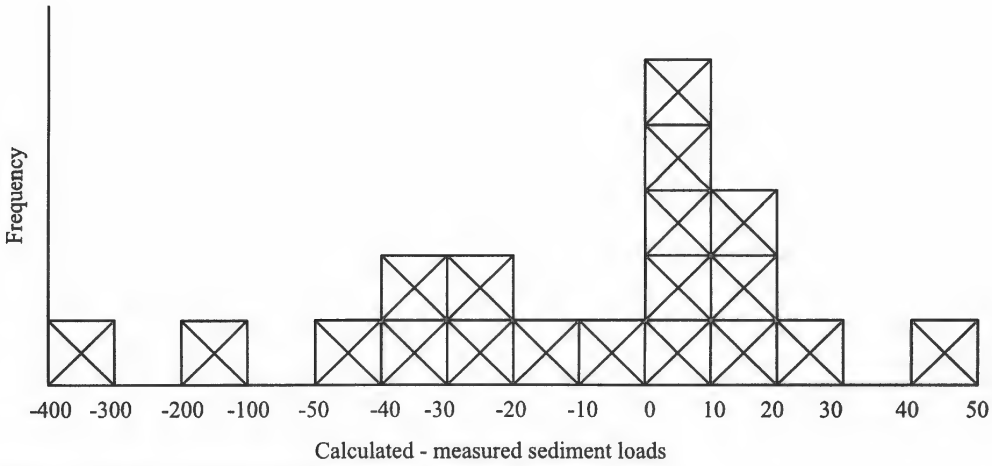

Figure 4. Distribution of errors at Pete King Stream.

that one of the model assumptions (Cline, et al., 1981) states that sediment yield can be effectively modeled using average precipitation values. However, at Pete King Stream, the correlations between mean and maximum stream discharge and the errors for the full dataset were extremely low (R^2 = -0.06). When the two outliers were eliminated, a slight correlation was shown: R^2 = 0.14 and 0.18 for mean and maximum discharge, respectively.

To test the relationship between precipitation and the errors, data (annual and maximum monthly precipitation) from monitoring stations closest to the two watersheds was obtained. For reference, the Fenn and Pierce station data were compared to the Pete King and Lolo watersheds, respectively.

The relationship between maximum monthly precipitation and the model errors was nonexistent (R^2 = 0.007 and 0.01); correlations between annual precipitation and errors were slightly higher (R^2 = 0.13 and 0.07 at Pete King and Lolo), but still remained unimportant.

Summary

Comparisons between measured and model sediment yields at Lolo Creek show that the WATBAL model consistently underestimates the amount of sediment reaching the stream. In fact, not once did WATBAL overestimate sediment loading. Analyses comparing the differences between model and measured sediment yield indicate that stream discharge, particularly maximum stream discharge, is a primary factor in explaining the magnitude of the errors.

The differences between model and measured sediment yields at Pete King Stream cannot simply be explained by stream discharge, even though there are slight correlations. However, with the exception of those years which contributed extremely high amounts of sediment due to catastrophic road failures, the errors are distributed (approximately) normally about zero.

One model weakness is the manner in which WATBAL treats precipitation—particularly storm intensity. Correlations between model error and precipitation are extremely low (R^2 = 0.007—0.13); however, correlations between error and stream discharge are much higher (R^2 = 0.14—0.60). The reason for this difference may be that the effects of intense storms are often lost within monthly/annual precipitation volumes, whereas discharge is more directly related to storm intensity. The catastrophic failures of roads during 1979 and 1987 illustrate this relationship clearly—high discharge and sediment yield, but average to below average precipitation volumes for the months in question.

A closer examination of the WATBAL Technical User Guide (Patten, 1989) and the Guide for Predicting Sediment Yields from Forested Watersheds (Cline, et al., 1981) revealed four other potential sources of error. 1) Both publications make the assumption that surface erosion is insignificant on undisturbed forests—even during intense rains. 2) The WATBAL model reduces erosion rates for roads based upon the road's age. While this assumption may be valid during normal hydrologic conditions, the occurrence of road-related mass movement events increased with increasing road age during the exceptionally wet winter/spring of 1995/96 (Jones, 1996). 3) The calculation of road-related erosion mitigation (in percent reduction of erosion) is directly, rather than proportionally, cumulative. For example, if a rep-rap fill will reduce erosion by 50% and a seed and fertilizer application 25%, WATBAL calculates a 75% erosion reduction rather than 50% plus 25% of the remainder (12.5%) for a total reduction of 62.5%. 4) Finally, the size of an individual landtype unit, 8.1—81 hectares (20—200 acres), requires averaging which can potentially contribute to significant error. If nothing else, slope length is not constant from one side of a landtype unit to the other. Slope angle probably is not a constant either, and both exert considerable influence upon surface erosion calculations.

Conclusions

The implications of this study are 1) the limitations built into WATBAL by the "Guide for Predicting Sediment Yields from Forested Watersheds" (Cline, et al., 1981) are a primary reason for differences between measured and predicted sediment yields, 2) model validation should be an integral part of sediment yield modeling, and 3) if used as a planning tool, WATBAL output must be carefully evaluated. At Lolo Creek, sediment yields have been invariably underestimated, potentially setting the stage for long-term damage to the stream. At Pete King Stream, WATBAL is effectively predicting an average sediment yield (if catastrophic road failures are ignored). This statement must be further qualified, however, because the differences between predicted and measured sediment yields may be as high as an order of magnitude. Thus, a single road failure can deliver 10 years of average annual sediment supply into a stream at once. Such an event can severely impact fisheries for a number of years (Megahan, et al., 1992).

A possible solution to a number of the limitations of WATBAL would be to re-build the model within a geographic information system (GIS). Some of the advantages include:

a) The scale of the minimum mapping unit could be increased to, for example, a 30x30 meter cell.

b) Much of the important physical data is already available, for example, digital elevation models (DEM), soils maps, and Landsat imagery.

It is important to note that cell-by-cell calculations of slope angle and slope length are possible—rather than using averages for large areas (Hickey, et al., 1994).

c) The database could be easily updated using Landsat imagery.

d) Drainage paths and directions can be calculated and included in the model.

e) The relatively generic database structure allows the use of both average annual and discrete event modeling. As new techniques and improved software are developed, the models used in the Forest can be modified without having to alter the original data—only how it is used.

In summary, regardless of the type of model used, the limitations inherent in all models should be taken into consideration. In the case of the WATBAL model, average sediment yields are calculated—therefore, the inherent limitation is that 50% of the time, sediment yields are underestimated. Thus, forest management plans should be based upon higher than average sediment yields. To draw an engineering analogy, bridges are not built to withstand average (yearly) stream discharges, but to tolerate 50 or 100 year flood levels. Forest planning need not be based around such catastrophic events; however, tolerances for some above normal rainfall events (or years) should be included in planning considerations—i.e. using sediment yield values one standard deviation above normal.

Acknowledgements

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Note

The following article, "Breeding Bird Abundance and Habitat Relationships on a Private Industrial Forest in the Western Washington Cascades," by Thomas Bosakowski (pp. 244-253) is a corrected reprint of the same article printed in the May 1997 issue of *Northwest Science* (Vol. 71, No. 2, pp. 87-96) . The article, as it appeared in Vol. 71, No. 2, had an incorrect graphic inserted for Figure 1. The article is reprinted in this issue with the proper figure.

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Breeding Bird Abundance and Habitat Relationships on a Private Industrial Forest in the Western Washington Cascades

Abstract

Surveys were conducted to determine the presence, relative abundance, and habitat relationships of the breeding bird community on a private industrial forest (21,600 ha) in western Washington. A total of 284 and 299 point counts (8 min duration) were established in 1995 and 1996, respectively, along unpaved logging roads separated by a minimum distance of 240 m. The counts were performed twice, at least 10 days apart. A total of 9,491 detections of 78 species of breeding birds were detected at point count stations during the survey period with 40 species having >30 detections. A GIS analysis of forest habitat types was run for a 100-m radius circle centered on each survey point. Of 61 species tested by multiple regression analysis, significant positive regressions were revealed for the following habitat types: mature conifer habitat (>45 yr) for 32 species, pole-sized conifer habitat (27-44 yr) for 27 species, sapling-sized conifer habitat (6-26 yr) for 38 species, recent clearcut habitat (0-5 yr) for 32 species, non-forested habitat (including open water) for 20 species, and alder-hardwood habitat (all ages) for 19 species. Overall, the GIS-habitat/mutiple regression models demonstrated that all successional stages on an industrial forest were important to different groups of species within the breeding bird community. Species richness was equal or greater than observed in studies conducted on federal lands in the Pacific Northwest and suggested that industrial forests can be managed to make an important contribution to regional biodiversity of breeding birds.

Introduction

During the past 40 years, logging in Washington and Oregon has converted 80 to 90 percent of the original mature and old-growth forest into a complex mosaic of early and late-successional forest (Harris 1984, Meslow et al. 1981, Spies and Franklin 1988, Bolsinger and Waddell 1993). Previous breeding bird surveys in the southern Washington Cascades (Manuwal and Huff 1987, Manuwal 1991) and the central Oregon Coast Range (McGarigal and McComb 1992) were conducted on National Forest lands which generally receive different and less-intensive silvicultural treatments, but yet have a propensity for higher levels of forest fragmentation (Franklin and Foreman 1987, Li et al. 1993). Forest fragmentation is less of a concern for industrial forests because high harvest rates have resulted in nearly complete conversion of old forests into plantations (Spies and Franklin 1988) and the practice of clearcutting large blocks leaves few fragments (Lehmkuhl et al. 1991). Because of these fundamental differences in forest management, the characterization of breeding bird populations on private industrial forest land should be investigated to examine the potential of these lands to contribute to regional conservation and biodiversity efforts. Virtually all of the previous studies on breeding bird communities in the Pacific Northwest have been conducted on federal lands.

In this study, surveys were conducted to determine the presence, relative abundance, and habitat relationships of the breeding bird community on a private industrial forest in the western Washington Cascade range. The surveys were part of a monitoring plan which was required under a multi-species Habitat Conservation Plan (HCP) implemented by the landowner. However, the results of the study have valuable implications for monitoring populations and predicting habitat suitability on other northwestern industrial forests.

Study Area

The study area was the Mineral Tree Farm in Lewis County Washington, an industrial tree farm of about 21,600 ha in total area which is owned and operated by the Murray Pacific Corporation (Tacoma, WA). The tree farm is located along the western edge of the Southern Cascade Physiographic Province and ranges in elevation from about 300 to 1640 m. Approximately 19,600 ha of the tree farm are capable of supporting forest growth, with the remaining area containing rocky ridgetops, alpine meadows, cliff/talus slopes, roads, brush, standing water, and gravel pits. The timberlands fall within the *Tsuga heterophylla* Forest Zone (Franklin and Dyrness 1984), which is dominated by Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*). Western redcedar (*Thuja*

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plicata) is locally abundant, and Pacific silver fir (*Abies amabilis*) and noble fir (*A. procera*) are present at higher elevations. Commercial timber production is the dominant land use on the Mineral Tree Farm, which is characterized by stands of various age classes including recent clearcuts (0-5 yr; 12%), saplings (6-26 yr; 43%), pole forest (27-45 yr; 28%), and commercially mature forest (>45 yr; 15%). Isolated stands of old-growth forest (>250 yr) occurs on less than 2% of the tree farm. The area is characterized by a mild, wet maritime climate. Precipitation occurs mainly in winter and averages 180 to 360 cm annually.

Methods

We used the "extensive point count" technique to quantitatively sample the breeding bird community (Ralph et al. 1993). A total of 284 and 299 point counts were surveyed in 1995 and 1996, respectively, with 248 locations repeated in both years and a total of 330 different locations. Specifically, a fixed-distance point count was used, whereby all birds seen or heard during an 8-minute period were recorded (Manuwal and Huff 1987), if within 100 m of each observation point. Unlimited distance point counts are not recommended for most survey needs, especially where loud streams can reduce detection levels of birds (McGarigal and McComb 1992). All surveys were conducted by the author and two other qualified field biologists. During surveys, we also recorded aerial foragers that flew within 100 m above the ground (swifts, swallows, hawks, etc.) since they were probably using the point count habitat for foraging. Ralph et al. (1993) recommended that stations should only be sampled once a season for most breeding bird surveys, unless the goal is to get good estimates of small or rare habitats. We conducted two separate visits at each survey station to improve the probability of detection due to variables such as weather, nesting phenology, and time of migration. In 1995, the first visit was conducted from 15 May to 1 June. The second visit was conducted from 6 June to 29 June. In 1996, the first visit was conducted from 21 May to 31 May. The second visit was conducted from 3 June to 27 June. At least 10 days elapsed between visits during each year.

Surveys were usually conducted during fair weather, but occasionally were done during intermittent drizzle, misting, and light fog which did not decrease normal levels of bird activity and singing. Surveys were cancelled during significant rain, fog, or if winds exceeded 20 kmph. All surveys were conducted from sunrise to mid-morning hours, but did not go beyond 10:00 as recommended (Ralph et al. 1993). All field identifications, nomenclature, and taxonomy are consistent with Peterson (1990). A four-letter code (acronym) for each species was used in the field to record birds on original data forms as recommended by Ralph et al. (1993).

Point counts were established along driving routes to improve survey efficiency and were separated by a minimum distance of 240 m (0.15 mile) as recommended by Ralph et al. (1993) to avoid duplication of counting effort. The points were all located on unpaved logging roads (secondary and tertiary) as recommended by Ralph et al. (1993) and were marked with green vinyl streamers which indicated the site number for replicate visits to the site. The routes were systematically established throughout the tree farm in nearly all drainages and elevations containing driveable dirt roads.

A vector-based (ARC/INFO) Geographic Information System (GIS) was used to delineate six habitats as follows: commercially mature conifer (45+ years), pole conifer (27-44 years), sapling conifer (6-26 years), alder-hardwood (all ages), recent clearcut (0-5 years), and non-forested land (open water, rock, brush). Survey points were selected to provide an equivalent sample size from each forest habitat type as well as along wetlands, streams, and uplands. Each point was given a unique identification number and was plotted on 1:24,000 scale GIS color habitat maps of the Mineral Tree Farm.

After the surveys were completed, the data for each point count station were entered into a computer database spreadsheet (Lotus 1-2-3, Cambridge, Massachusetts). The data sets from the two years were combined and the total number of sites occupied by each species was calculated (% of 330 total stations occupied).

Due to previous timber harvesting patterns, relatively few points were placed in single forest habitat types, so sites were usually a composite of several different habitats. All point count locations from field maps were digitized into the GIS and habitat areas within a 100 m radius were calculated. A multiple regression analysis using ordinary least squares was used to determine relationships between breeding birds (dependent

variable) and corresponding habitat measures as independent variables. There are no underlying assumptions on the distribution of the independent variables in multiple regression analysis (Kerlinger and Pedhazur 1973), and therefore, data transformations were not applied to the GIS habitat data. In order to avoid problems with normality among the independent variables (bird counts), abundance values were converted to a non-parametric scale (presence =1, absence = 0) as used in logistic regression analysis (Robbins et al. 1989). This also eliminated common biases in abundance counts due to differences in species-specific breeding densities and territory sizes. A separate full-model (all variables included) multiple regression analysis was run for each species so that they would be directly comparable to each other and because stepwise procedures have recently been criticized for use in ecology by many investigators (see review by James and McCulloch 1990). All statistical analyses were run on a personal computer using version 5.03 of NCSS (Number Cruncher Statistical System, Kaysville, Utah). Results are presented only for breeding birds with at least one significant habitat regression ($p < 0.05$), but species habitat models with small sample sizes should be regarded with caution. One limitation of this model is that it may not completely compensate for species which nest and forage in different habitats (see Brown 1985 for examples), and therefore, the results reported herein should also be considered in light of the current knowledge of the nesting biology of the species.

Results

A total of 9,491 detections of breeding birds occurred during the two-year survey (Table 1). A total of 78 species of breeding birds were detected at point count stations over the two years. There were a total of 70 species observed in each year, although 16 species were only recorded in one of the two survey years. During the survey period, at least 40 species had >30 detections.

Survey Replication

Point counts were highly consistent between the two visits and between years for certain species (e.g., Hammond's flycatcher, Pacific slope flycatcher, winter wren, golden-crowned kinglet, varied thrush, song sparrow). For some permanent residents and early migrants, abundance was noticeably greater on the first visit, suggesting an earlier nesting phenology (e.g., blue grouse, northern flicker, black-throated gray warbler). Abundance was noticeably greater on the second visit for some species of late migrants (e.g., willow flycatcher, Swainson's thrush, warbling vireo, black-headed grosbeak). In both 1995 and 1996, 14 species were detected on only one of the two visits, thereby showing the value of replicating counts at least twice during the breeding season (at least 10 days apart).

Relative Abundance

Of 78 species detected on the survey, 10 were detected at more than 50 percent of the survey sites, including: Pacific slope flycatcher, winter wren, dark-eyed junco, American robin, Swainson's thrush, chestnut-backed chickadee, golden-crowned kinglet, Stellar's jay, varied thrush, and hermit warbler. Another 13 species were detected at between 20 and 50 percent of survey sites and six species were detected at 10 to 20 percent of survey sites. Three candidates for state-listing in Washington were also found during the survey, including: Vaux's swift (40 detections), pileated woodpecker (34), and western bluebird (3).

Habitat Relationships

A full-model multiple regression analysis was conducted with all six independent variables (GIS forest habitat types) for each breeding bird species. A total of 61 species had at least one 1 to 6 significant regressions with the six habitats used in the analysis (Table 2). For mature conifer habitat (>45 yr), significant positive regressions were revealed among 32 bird species. For pole-sized conifer habitat (27-44 yr), significant positive regressions were revealed among 27 bird species. For sapling-sized conifer habitat (6-26 yr), significant positive regressions were revealed among 38 species. For recent clearcut habitat (0-5 yr), significant positive regressions were revealed among 32 species. For non-forested habitat (including open water), significant positive regressions were revealed among 20 species. For alder-hardwood habitat (all ages), significant positive regressions were revealed among 19 species.

Discussion

This survey documented a diverse breeding bird community of 78 species occurring on the Mineral

TABLE 1. Breeding bird survey results from an industrial tree farm in the western Washington Cascades, Lewis County (284 point counts in 1995 and 299 point counts in 1996).

Species	Species Code	1995 Total Number Visit #1	1995 Total Number Visit #2	1996 Total Number Visit #1	1996 Total Number Visit #2	Total Number of Detections	Percent of Stations Occupied
mallard *Anas platyrhynchos*	MALL	4	1	0	8	13	0.6
common merganser *Mergus merganser*	COME	0	0	0	1	1	0.3
sharp-shinned hawk *Accipiter striatus*	SSHA	1	1	0	0	2	0.6
Cooper's hawk *Accipiter cooperii*	COHA	0	0	0	1	1	0.3
red-tailed hawk *Buteo jamaicensis*	RTHA	3	11	1	3	18	4.8
American kestrel *Falco sparverius*	AMKE	2	0	0	1	3	0.9
blue grouse *Dendragapus obscurus*	BLGR	36	18	41	29	124	24.9
ruffed grouse *Bonasa umbellus*	RUGR	13	3	1	0	17	4.8
band-tailed pigeon *Columba fasciata*	BTPI	8	4	10	4	26	5.1
common snipe *Gallinago gallinago*	COSN	0	0	3	1	4	0.6
great horned owl *Bubo virginianus*	GHOW	0	0	1	2	3	0.3
northern pygmy-owl *Glaucidium gnoma*	NPOW	2	1	0	1	4	1.2
common nighthawk *Chordeiles minor*	CONI	0	3	0	2	5	1.5
Vaux's swift *Chaetura vauxi*	VASW	11	0	25	4	40	3.6
rufous hummingbird *Selasphorus rufus*	RUHU	13	8	13	27	61	15.0
red-breasted sapsucker *Sphyrapicus ruber*	RBSA	10	5	4	7	26	5.7
red-naped sapsucker *Sphyrapicus nuchalis*	RNSA	0	2	0	0	2	0.6
downy woodpecker *Picoides pubescens*	DOWO	3	0	1	2	6	1.8
hairy woodpecker *Picoides villosus*	HAWO	36	35	51	23	145	29.6
northern flicker *Colaptes auratus*	NOFL	31	18	38	17	104	22.5
pileated woodpecker *Dryocopus pileatus*	PIWO	11	13	2	8	34	7.8
olive-sided flycatcher *Contopus borealis*	OSFL	15	22	20	16	73	14.4
western wood-pewee *Contopus sordidulus*	WWPE	1	0	1	2	4	1.2
willow flycatcher *Empidonax traillii*	WIFL	13	51	28	79	171	23.4
Hammond's flycatcher *Empidonax hammondii*	HAFL	23	22	16	24	85	13.8
Pacific slope flycatcher *Empidonax difficilis*	PSFL	241	249	212	271	973	83.8
tree swallow *Tachycineta bicolor*	TRSW	5	11	11	4	31	3.6
violet-green swallow *Tachycineta thalassina*	VGSW	4	6	1	4	15	2.1
no. rough-winged swallow *Stelgidpteryx serripennis*	NRSW	1	0	0	0	1	0.3
barn swallow *Hirundo rustica*	BASW	3	2	0	0	5	1.2
gray jay *Perisoreus canadensis*	GRJA	18	31	29	31	109	20.4
Steller's jay *Cyanocitta stelleri*	STJA	91	74	109	93	367	57.5
American crow *Corvus brachyrhynchos*	AMCR	4	2	2	2	10	0.9
common raven *Corvus corax*	CORA	4	4	11	11	30	5.7
black-capped chickadee *Parus atricapillus*	BCCH	1	0	5	0	6	0.9
chestnut-backed chickadee *Parus rufescens*	CBCH	79	67	146	133	425	61.4
red-breasted nuthatch *Sitta canadensis*	RBNU	48	33	42	34	157	31.1
brown creeper *Certhia americana*	BRCR	6	11	5	9	31	8.4
Bewick's wren *Thryomanes bewickii*	BEWR	1	0	0	0	1	0.3
house wren *Troglodytes aedon*	HOWR	2	1	0	1	4	1.2
winter wren *Troglodytes troglodytes*	WIWR	241	240	222	207	910	80.8
American dipper *Cinclus mexicanus*	AMDI	0	0	4	4	8	1.8
golden-crowned kinglet *Regulus satrapa*	GCKI	115	110	94	82	401	59.6
ruby-crowned kinglet *Regulus calendula*	RCKI	2	0	0	0	2	0.6
western bluebird *Sialia mexicana*	WEBL	2	1	0	0	3	0.3
Townsend's solitaire *Myadestes townsendi*	TOSO	17	6	9	16	48	9.9
Swainson's thrush *Catharus ustulatus*	SWTH	92	192	123	172	579	69.5
hermit thrush *Catharus guttatus*	HETH	15	17	45	42	119	20.4

continued, next page

Table 1, continued

Species	Species Code	1995 Total Number Visit #1	1995 Total Number Visit #2	1996 Total Number Visit #1	1996 Total Number Visit #2	Total Number of Detections	Percent of Stations Occupied
American robin *Turdus migratorius*	AMRO	89	66	74	100	329	55.7
varied thrush *Ixoreus naevius*	VATH	150	150	170	177	647	71.0
cedar waxwing *Bombycilla cedrorum*	CEWA	0	6	3	4	13	2.1
solitary vireo *Vireo solitarius*	SOVI	0	0	0	2	2	0.3
Hutton's vireo *Vireo huttoni*	HUVI	11	13	13	1	38	10.2
warbling vireo *Vireo gilvus*	WAVI	55	97	48	82	282	40.4
orange-crowned warbler *Vermivora celata*	OCWA	23	15	17	10	65	12.3
yellow warbler *Dendroica petechia*	YEWA	0	3	0	1	4	0.9
yellow-rumped warbler *Dendroica coronata*	YRWA	8	4	17	7	36	4.2
black-throated gray warbler *Dendroica nigrescens*	BGWA	67	33	45	39	184	27.2
Townsend's warbler *Dendroica townsendi*	TOWA	6	1	8	1	16	3.3
hermit warbler *Dendroica occidentalis*	HEWA	84	100	121	94	399	52.4
MacGillivray's warbler *Oporornis tolmiei*	MGWA	76	82	77	73	308	42.5
common yellowthroat *Geothlypis trichas*	COYE	0	1	0	0	1	0.3
Wilson's warbler *Wilsonia pusilla*	WIWA	87	73	72	66	298	47.0
western tananger *Piranga ludoviciana*	WETA	53	72	57	42	224	39.5
black-headed grosbeak *Pheucticus melanocephalus*	BHGR	14	28	22	29	93	18.9
rufous-sided towhee *Pipilo erythrophthalmus*	RSTO	21	20	26	24	91	17.7
fox sparrow *Passerella iliaca*	FOSP	0	0	1	0	1	0.3
song sparrow *Melospiza melodia*	SOSP	51	52	59	57	219	31.4
Lincoln's sparrow *Melospiza lincolnii*	LISP	6	1	3	0	10	1.5
white-crowned sparrow *Zonotrichia leucophrys*	WCSP	23	33	37	36	129	18.9
dark-eyed junco *Junco hyemalis*	DEJU	149	206	186	228	769	78.4
red-winged blackbird *Agelaius phoeniceus*	RWBL	3	8	4	1	16	1.5
brown-headed cowbird *Molothrus ater*	BHCO	1	0	1	0	2	0.6
red crossbill *Loxia curvirostra*	RECR	0	0	16	18	34	2.7
purple finch *Carpodacus purpureus*	PUFI	4	2	0	1	7	1.8
pine siskin *Carduelis pinus*	PISI	3	1	10	18	32	6.3
American goldfinch *Carduelis tristis*	AMGO	7	4	0	1	12	2.7
evening grosbeak *Coccothraustes vespertina*	EVGR	9	12	1	1	23	4.5
Totals		2228	2358	2414	2491	9491	

Tree Farm, with 40 species having >30 detections. Previous surveys in the southern Washington Cascades (Manuwal and Huff 1987) were on National Forest lands and detected only 46 species of breeding birds, even though young (42-75 yr), mature (105-165), and old-growth stands (250+ yr) were surveyed. That study used fewer point counts (42), but more replicates which may partially explain their lower total number of species. We also included wetlands and clearcuts in our sampling which undoubtedly helped to increase species richness for the tree farm. Surveys in Oregon (McGarigal and McComb 1992) found 55 breeding bird species at 96 point counts (only 10 species having >30 detections), but these surveys were limited to mature coniferous and hardwood forests. Surveys in Northern California/Southern Oregon (Ralph et al. 1991) found a similar number of species (71) in Douglas-fir/hardwood stands. Overall, the Mineral Tree Farm had a high species richness compared to previous Northwest investigations and contained virtually all of the breeding bird species expected for its geographic location.

The GIS-habitat/mutiple regression models demonstrated that all successional stages on an

TABLE 2. Results of multiple regression analysis of breeding bird occupancy versus GIS-habitat classes in a 100 m radius circle around point counts. Data listed under habitats are standardized beta coefficients (* indicates a probability < 0.05 that the slope of the regression is zero). R^2 is the overall adjusted r-squared value for the full-model multiple regression equation (P is the probability of the slope of the equation equalling zero).

Species Code	mature conifer >45 yr	pole conifer 27-44 yr	sapling conifer 6-26 yr	recent clearcut 0-5 yr	non-forested habitats	alder/ hardwoods	R^2	P
MALL	-0.031	-0.016	0.129*	-0.010	0.102	-0.022	0.018	0.092
RTHA	0.222*	0.018	-0.004	0.076	0.032	0.084	0.066	0.001
AMKE	-0.043	-0.018	0.064	0.167*	-0.001	-0.027	0.015	0.120
BLGR	0.276*	0.154*	0.137*	0.236*	0.027	0.043	0.254	0.001
RUGR	-0.021	0.226*	0.164*	0.020	-0.009	-0.009	0.072	0.001
BTPI	0.093	0.100	0.144*	0.086	-0.050	-0.030	0.046	0.002
VASW	0.111*	0.024	0.098	0.098	0.007	-0.038	0.031	0.018
NPOW	0.058	0.055	-0.026	0.038	-0.021	0.152*	0.021	0.062
RUHU	0.141*	0.098	0.197*	0.166*	0.059	0.020	0.142	0.001
RBSA	-0.030	0.096	0.246*	0.100	0.009	-0.052	0.075	0.001
DOWO	0.048	0.003	0.066	0.005	0.019	0.163*	0.026	0.031
HAWO	0.188*	0.096*	0.124*	0.414*	0.039	0.147*	0.359	0.001
NOFL	0.076	0.059	0.214*	0.380*	0.085	0.028	0.269	0.001
PIWO	0.184*	0.120*	0.022	0.146*	0.040	-0.017	0.083	0.001
OSFL	0.134*	0.001	0.249*	0.265*	0.028	-0.086	0.185	0.001
WIFL	0.056	0.048	0.267*	0.347*	0.078	0.073	0.272	0.001
HAFL	0.352*	-0.013	0.012	0.266*	0.017	0.005	0.237	0.001
PSFL	0.365*	0.412*	0.342*	0.294*	0.088*	0.179*	0.844	0.001
TRSW	-0.030	0.019	0.194*	0.045	0.135*	-0.026	0.059	0.001
VGSW	0.017	0.024	0.101	0.003	0.194*	-0.020	0.048	0.002
BASW	-0.012	0.095	-0.042	0.113*	0.129*	-0.033	0.023	0.049
GRJA	0.164*	0.247*	0.200*	0.134*	-0.016	0.070	0.204	0.001
STJA	0.217*	0.316*	0.400*	0.252*	0.068	0.091	0.571	0.001
AMCR	-0.042	-0.014	-0.005	-0.022	0.388*	0.058	0.142	0.001
CORA	0.110*	0.136*	0.098	0.053	-0.011	0.039	0.048	0.002
BCCH	-0.035	0.028	-0.024	0.047	0.186*	0.097	0.035	0.010
CBCH	0.373*	0.337*	0.314*	0.190*	0.104*	0.110*	0.626	0.001
RBNU	0.418*	0.128*	0.107*	0.254*	0.018	0.063	0.376	0.001
BRCR	0.314*	0.098	-0.013	0.071	0.061	0.007	0.125	0.001
HOWR	0.024	-0.022	-0.026	0.081	0.045	0.178*	0.032	0.015
WIWR	0.356*	0.435*	0.351*	0.252*	0.071*	0.177*	0.818	0.001
AMDI	0.075	0.121*	-0.034	0.032	0.004	0.087	0.019	0.076
GCKI	0.448*	0.418*	0.294*	0.102*	0.005	0.102*	0.657	0.001
TOSO	0.232*	0.053	0.032	0.253*	-0.022	-0.035	0.144	0.001
SWTH	0.276*	0.304*	0.431*	0.253*	0.116*	0.125*	0.695	0.001
HETH	0.200*	0.136*	0.297*	0.098	0.082	-0.080	0.220	0.001
AMRO	0.240*	0.222*	0.262*	0.377*	0.167*	0.132*	0.577	0.001
VATH	0.347*	0.389*	0.402*	0.184*	0.078*	0.101*	0.718	0.001
CEWA	0.087	-0.026	0.116*	0.017	0.029	0.039	0.018	0.088
HUVI	0.066	0.232*	0.145*	0.099	-0.039	0.061	0.108	0.001
WAVI	0.039	0.141*	0.397*	0.264*	0.146*	0.221*	0.465	0.001
OCWA	-0.001	0.074	0.370*	0.107*	0.067	-0.043	0.175	0.001
YRWA	0.106	-0.002	0.176*	0.055	0.032	-0.043	0.047	0.002
BGWA	0.150*	0.405*	0.144*	0.065	0.028	0.257*	0.358	0.001
TOWA	0.134*	0.229*	0.032	-0.030	-0.028	-0.027	0.060	0.001
HEWA	0.416*	0.378*	0.196*	0.182*	0.076*	0.057	0.561	0.001
MGWA	0.112*	0.034	0.417*	0.398*	0.100*	0.091*	0.504	0.001
WIWA	0.146*	0.268*	0.431*	0.186*	0.098*	0.099*	0.487	0.001

continued, next page

TABLE 2, continued

Species Code	mature conifer >45 yr	pole conifer 27-44 yr	sapling conifer 6-26 yr	recent clearcut 0-5 yr	non-forested habitats	alder/ hardwoods	R^2	P
WETA	0.361*	0.145*	0.193*	0.294*	-0.044	0.177*	0.448	0.001
BHGR	0.019	0.139*	0.166*	0.298*	0.084	0.127*	0.213	0.001
RSTO	0.061	0.026	0.203*	0.318*	0.065	0.092	0.209	0.001
SOSP	0.042	0.012	0.339*	0.389*	0.187*	0.059	0.410	0.001
LISP	-0.020	-0.004	0.016	0.039	0.376*	-0.048	0.132	0.001
WCSP	0.089	0.021	0.134*	0.425*	0.079	0.025	0.261	0.001
DEJU	0.237*	0.328*	0.388*	0.424*	0.120*	0.102*	0.795	0.001
RWBL	-0.044	0.042	0.145*	0.008	0.115*	-0.032	0.030	0.019
RECR	0.132*	0.022	0.063	0.065	0.020	-0.034	0.022	0.052
PUFI	-0.048	-0.026	0.088	0.022	0.244*	0.080	0.077	0.001
PISI	0.223*	0.049	0.105	0.098	-0.055	-0.045	0.080	0.001
AMGO	0.000	0.085	-0.024	0.056	0.051	0.274*	0.085	0.001
EVGR	0.154*	0.148*	0.006	0.073	0.041	-0.042	0.051	0.001

industrial forest were important to different groups of species within the breeding bird community. Among the species that tended to be specialists (only 1 to 3 significant regressions), there were four distinct patterns that separated them from generalist species. Late successional species had their greatest affinity with mature conifer habitat (Fig. 1a). This group included two snag-dependent species: Vaux's swift and brown creeper, which require snags for nesting, roosting, or foraging (Brown 1985), as well as conifer seed-eaters that need to forage among mature mast-producing conifers (pine siskin, evening grosbeak, and red crossbill), and a large raptor which requires tall canopy trees for nest placement (red-tailed hawk).

Mature forest/edge species (Fig. 1b) differed from late-successional species by virtue of the inclusion of clearcut habitat with mature conifer habitat. This group included two snag-dependent species which typically inhabit late-successional forest: pileated woodpecker and red-breasted nuthatch (Brown 1985; Bull et al. 1986). The association of pileated woodpecker and red-breasted nuthatch with mature conifer forest and clearcuts was not due to a correlation between these two habitats ($r = -0.12$). Instead, it is possible that they were attracted to clearcut edges because of the higher levels of blowdowns, damaged trees, and mortality that can occur here (Norse 1990), as well as by snags, residual trees, logging slash, and stumps which were left behind in recent clearcuts. Bull et al. (1986) found that pileated woodpeckers foraged 36% of the time on downed logs and 29% in snags. Bull and Meslow (1977) also determined that 14% of feeding sites on dead wood were on stumps. In addition, Smith (1986) noted that damaged trees can produce large "distress crops" of seeds, and therefore, red-breasted nuthatches may also be attracted by local cone crop abundance along recent clearcut edges. Also in this group were three perch-hunting insectivores: olive-sided flycatcher, Hammond's flycatcher, and Townsend's solitaire, which are known to prefer forest-edge habitat (Brown 1985; Sharp 1992).

Early successional species (Fig. 1c) showed a decreasing trend of association with the successional stages, with the greatest affinity for clearcut and sapling habitats. This group included several ground foragers (white-crowned sparrow, song sparrow, and rufous-sided towhee), four shrub/sapling foragers (willow flycatcher, black-headed grosbeak, orange-crowned warbler, yellow-rumped warbler), and one open-terrain raptor (American kestrel).

As would be expected, the GIS-habitat models for alder/hardwood species (Fig. 1d) showed little association with conifer habitats, regardless of successional stage. This group included four cavity-nesters (downy woodpecker, house wren, northern pygmy-owl, and black-capped chickadee) with well-known affinities for deciduous or mixed conifer-hardwood stands (Brown 1985; Sharp 1992). American goldfinch is a seed-eater known to inhabit alder or other hardwood types

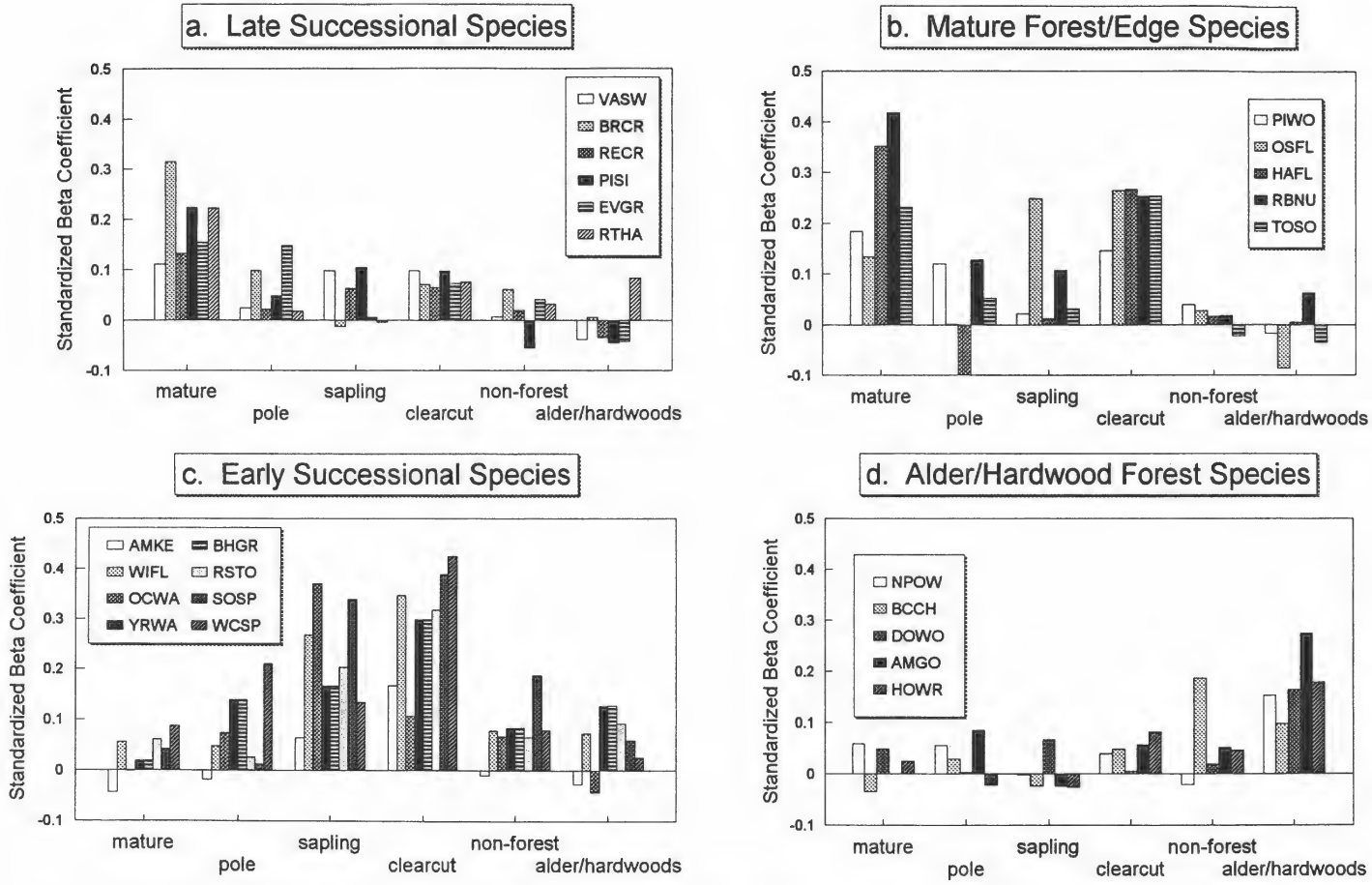

Figure 1. Groups of breeding bird species with similar habitat correlations from the GIS-habitat/multiple regression model (data represent standardized beta coefficients from Table 2). Species codes are given in Table 1.

(Brown 1985). None of these species were abundant because of the dominance of conifers on the Mineral Tree Farm.

Most of the 32 species that were significantly correlated with mature conifer in the GIS-habitat models were also observed to attain high abundance levels in mature and old-growth stands in other Northwest studies (Manuwal and Huff 1987, Manuwal 1991, Ralph et al. 1991). These strong similarities validate the utility of the GIS-habitat/multiple regression model which was developed for this study, as well as emphasize the value of maintaining mature forest habitat on private industrial forests for breeding birds. On the Mineral Tree Farm, mature conifer stands (>45 yrs) usually had higher densities of snags and remnant old-growth trees ("old-growth legacies"), than pole stands because of "sloppy clearcutting" and "high-grading" practices which were the norm before 1930 (McKelvey and Johnston 1992). Since that time, a chronic shortage of snags and large residual trees has occurred in clearcut units with the advent of "modern" intensive silviculture (Neitro et al. 1985). Intensive site preparation, concerns for worker safety, and salvage for wood chips and firewood have all contributed to a shortage of cull trees, snags, and residual trees in the Pacific Northwest (Neitro et al. 1985).

To mitigate for this predicted loss to wildlife diversity, special forest management prescriptions for the Mineral Tree Farm were developed in their HCP. These prescriptions require 30 m no-harvest buffers for wetlands and fish-bearing streams, 15 m buffers along approximately 59% of non-fish-bearing streams, and large quotas for snag/green-tree retention (i.e., 10 snags and 10 green trees must be left per ha of clearcut). No-harvest riparian buffer zones have been shown to retain most of the breeding bird species two years after clearcutting an area (Triquet et al. 1990). In addition, higher snag densities on clearcuts have been shown to produce a higher density and species richness of cavity-nesting birds (Schreiber and deCalesta 1992). The preferred use of uplands by many forest breeding birds in Oregon (McGarigal and McComb 1992) suggests that it is also important to maintain residual trees (seed trees, culls, and leave trees), snags, and no-harvest reserve areas in upland areas as well. If properly managed, industrial forests can make an important contribution to regional biodiversity and conservation of breeding birds.

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The Future Is Now: Biological Monitoring To Ensure Healthy Waters[1]

"Can we afford clean water? Can we afford rivers and lakes and streams and oceans which continue to make life possible on this planet? Can we afford life itself? . . . These questions answer themselves."

Senator Edmund Muskie, 1972

Aquatic ecosystems embrace an interactive mosaic of environments extending from headwater streams and meadows through mainstem rivers to the sea. This mosaic includes small streams and large rivers, shorelines and streambeds, terrestrial watersheds and groundwater aquifers. Water, plants, animals, nutrients, debris, and by-products of human society move among these environments no matter what the political boundaries or legal constructs established without regard for the connections.

Because rivers integrate everything in their landscapes, the living organisms found in rivers tell us about the status and quality of their watersheds. Unfortunately, the story told in North America's rivers today is one of damaged landscapes and the historical tendency to undervalue our rivers. Now is the time for citizens and their government agencies to reverse this trend.

Through most of the twentieth century, national efforts to protect water and associated resources were defined by the 1899 Rivers and Harbors (or Refuse) Act, which was passed to control sewage and oil spills in navigable waterways. By 1970 it was obvious that we needed a new approach. With passage of PL 92-500, the 1972 Water Pollution Control Act Amendments (now referred to as the Clean Water Act), hope for change came in the form of one explicit, wide-ranging, and visionary statement: "The objective of this Act is to restore and maintain the chemical, physical and biological integrity of the Nation's waters."

Although progress has been made under this law in controlling point-source pollution (as from factories or wastewater treatment plants), other

[1]This article was excerpted from *Streamkeepers: Aquatic Insects as Biomonitors,* published by the Xerces Society, a conservation organization devoted to invertebrates and the preservation of critical biosystems worldwide. To order a copy of *Streamkeepers,* a book of color photographs and essays about the ecology of rivers, and the potential of aquatic insect monitoring for wild fish and watershed conservation, contact the Xerces Society at 4828 SE Hawthorne Boulevard, Portland, Oregon 97215; phone (503)-232-6639.

harm continues—nonpoint pollution (such as runoff from agricultural, forest, or urban areas); altered hydrological regimes; habitat destruction; and the introduction of exotic species. To break this pattern, we must now recognize and deal with the following facts:

- Water resources, especially their biological components, are in steep decline.
- Degradation stems from more than chemical contamination, yet conventional water-quality programs focus primarily on that one dimension. The biota of rivers offers a multidimensional view and a more effective analytical tool.
- Long-term success in protecting water resources means measuring their condition with biological criteria, that is, by monitoring the organisms (such as insects, fish, or plants) that inhabit our rivers and streams.
- The Clean Water Act establishes a clear objective, and science provides the tools, for protecting our waters, but the regulatory framework and its implementation have yet to catch up.

We must begin to track the condition of aquatic systems the way Wall Street tracks the economy with gauges like the index of leading economic indicators. Our biological index should be sensitive to many different characteristics of living communities, as economic indicators describe many different aspects of economies. A good biological index should be much broader than an indicator of commodity production (e.g., water, fish, shellfish) or a count of threatened and endangered species.

Using biological criteria to monitor and sustainably manage our aquatic resources is a vital necessity in the face of current trends. Native species are declining, and exotic species are invading waters throughout the United States. The proportion of aquatic organisms at risk of extinction is considerably higher than that of terrestrial organisms. For example, only 11 to 14 percent of birds, mammals, and reptiles are classed as rare to extinct, but *34 percent of the fish, 65 percent of the crayfish, and 75 percent of the freshwater mussels found in North America are included in that category.*

Fish consumption advisories continue to increase, affecting forty-five to forty-seven states each year. Shoreline, or riparian, corridors have been destroyed along most U.S. streams. Throughout North America, commercial fisheries that once produced tons of edible fish (salmon, bass, shad, etc.) for humans have declined—generally by more than 90 to 95 percent. In the Pacific Northwest, 214 native, naturally spawning Pacific salmon and steelhead stocks face a high or moderate risk of extinction, or are of special concern. Since 1910, naturally spawning salmon runs in the Columbia River have declined by more than 95 percent.

We now know that a principal reason for these widespread losses is landscape alteration; monitoring for chemical contaminants does not identify the consequences of these alterations. Priority lists of chemicals simply do not reflect ecological risks accurately. Point-source pollution controls do not effectively counter damages from nonpoint sources or the cumulative effects of multiple contaminants. Further, installing wastewater treatment and collector systems to comply with chemical standards may actually damage or even destroy many miles of stream channels and riparian corridors; the effects on local and regional biological integrity can be devastating.

The chemical-contaminant approach fails to diagnose or correct water resource problems caused by other human influences. In the process of logging, grazing, urbanization, and recreation, we alter habitat structure by removing woody debris or destroying quiet pools. We disrupt flow patterns with dams or constructed channels. We remove organic material from riparian corridors, and we change relationships among organisms by introducing exotics or overharvesting fish for sport or commerce.

Long-term protection of water resources requires that we focus on the living organisms that inhabit our rivers and streams, because the value of water resources to society comes from more that water quality and quantity. Humans depend on living waterways for many essential goods and services; waters that cannot support healthy biological communities are unlikely to support human society. Biological criteria provide the most effective markers of environmental quality and the most relevant guideposts for federal and state programs to protect society's economic and ecological interests.

One biological gauge is the index of biological integrity (IBI), first developed in 1981 for monitoring midwestern U.S. streams. Like economic indexes, an IBI consists of multiple measures

(called metrics), each describing one aspect of a site's biological condition. IBIs have been developed for stream fishes and benthic (bottom-dwelling) invertebrates throughout the world; other IBIs are being developed to assess the condition of wetlands. Terrestrial IBIs using plants, insects, and birds are being tested for use at decommissioned nuclear weapons sites and to measure the health of forest ecosystems.

Researchers choose particular measures to incorporate into IBIs because those measures reflect specific and predictable responses of organisms to human activities across a landscape. These responses behave somewhat like the dose-response relationships measured by toxicologists. An organism's response to a toxic compound varies with dose; similarly, biological responses at a site reflect the cumulative impacts of disturbance affecting that site. When plotted on a graph, these measured responses demonstrate ecological dose-response curves. Considered together, they describe the health of complex ecological systems. They also enable decision makers, resource managers, and citizens to predict the ecological consequences of particular human activities (such as logging, grazing, urbanization, or recreation).

To be useful as metrics in an IBI, the biological responses that researchers choose to record should be relatively easy to measure and interpret. They must increase or decrease as human influence increases; they should be sensitive to a range of biological stresses. Most important, they must be able to discriminate human-caused disturbance from the background of natural variability. Historically, biologists tried to measure everything. But in addition to being expensive and logistically impossible, measuring everything fails to focus on clear signals of human-caused degradation.

Key biological features should be tracked to detect changes in species, including the identity and number of species present in standard samples; ecological processes such as nutrient dynamics and energy flow through food webs; and the health of individuals, which influences survival and reproduction. These features provide a comprehensive picture of water resource condition—one that goes beyond the toxicity or extent of chemical pollutants. Benthic invertebrates and fish are particularly appropriate for use in an IBI. Invertebrates are abundant and easily sampled, and the species living in virtually any water body represent a diversity of morphological, ecological, and behavioral adaptations to their natural habitat. As humans alter watersheds and water bodies, shifts occur in taxa richness (number of kinds), species composition (identity of species), individual health, and feeding and reproductive relationships of fish and invertebrates.

Samples of invertebrates from one of the best streams in rural King County, Washington, for example, contain twenty-seven taxa of invertebrates; similar samples from an urban stream in Seattle contain only seven. The rural stream has eighteen taxa of mayflies, stoneflies, and caddisflies, the urban stream only two or three. When these and other metrics are combined in an index based on invertebrates, the resulting "benthic index of biological integrity" (B-IBI) provides a numeric description of the condition, or health, of a stream (Table 1). The B-IBI for the rural stream in King County was forty-three (the nine-metric index maximum is 45); that for the urban stream was 9 (the index minimum).

TABLE 1. Benthic indexes of biological integrity (B-IBI) for streams in King County, Washington, and in and near Grand Teton National Park, Wyoming.

Region	Land Use	B-IBI
King County, WA	Rural	43
	Urban	9
Grand Teton Region, WY	Little or no human activity	44
	Low to moderate recreation	41
	High recreation	28
	Urban	21

The B-IBI can also be used to compare sites in different areas. For example, nearly pristine areas in Grand Teton National Park have near-maximum B-IBIs. Streams with moderate levels of recreation in their watersheds have B-IBIs that are not significantly lower than those without human use, but places where recreation is heavy are clearly damaged. Urban streams in Jackson, Wyoming (near the National Park) are even more degraded, yet not as bad as urban streams in Seattle.

Thus this numeric index makes it possible to compare stream quality across geographic areas so that citizens as well as managers can establish priorities for protection and restoration. Multimetric

biological monitoring recognizes that the quantitative biological conditions that constitute health vary geographically because the underlying chemical, physical, and biological properties of streams vary geographically. Properly used, IBI is calibrated to account for that variation.

Biological monitoring and assessment ultimately provide objective descriptions of the condition of our waters. They diagnose and integrate chemical, physical, and biological impacts as well as their cumulative effects; they can serve many kinds of environmental and regulatory programs when integrated with chemical analyses and single-species toxicity testing in the laboratory; and they are cost effective. Most important, because biological monitoring is sensitive to different impacts of human activity, it offers greater protection to water resources than chemical testing alone can provide.

Biological monitoring provides a more economical and effective method for accomplishing the broad objective articulated in the Clean Water Act. We no longer need to implement the act as if crystal clear distilled water running down concrete conduits were its objective. The tools for effective biological monitoring and assessment are now available.

Protecting water quality goes beyond clear water, beyond protecting single desired species. Certain taxa may be valuable for commerce or sport, but these species do not exist in isolation. We cannot predict which organisms are critical to the persistence of commercial species or species we want for other reasons. Failing to protect phytoplankton, zooplankton, insects, higher plants, bacteria, or fungi ignores the key contributions of these taxa to healthy biotic communities. *No matter how important a particular species is to humans, it cannot persist outside the biological context that sustains it.*

Water law that exists today still reflects the needs of a young, uncrowded nation moving into a limitless frontier. One hundred and fifty years ago there was less scientific knowledge, societal values were different, and ample water was available. Times have changed, and our attitudes must too. Only an integrative approach within each level of government (EPA, Forest Service, Fish and Wildlife Service, Geological Survey), across levels of government (local, state, regional, national, international), and among citizen groups can protect water resources.

Perhaps the most important step toward real protection of the nation's waters is to stop talking about water quality and start formulating policy that protects the biological integrity of our rivers, streams, lakes, wetlands, and oceans. Let us adopt a broader concept of water; redefine societal goals based on that concept; forge partnerships among scientists, policymakers, resource managers, and citizens to attain those goals; revise the legal framework guiding water resource policy; and redouble our efforts to protect high quality waters and to restore those that are degraded.

Book Review

Metapopulations and Wildlife Conservation

Dale R. McCullough, ed., 1996, Island Press, Washington, DC, 429 pages ($55.00, Paper $28.00)

What is a metapopulation? How does metapopulation theory apply to our increasingly fragmented natural areas? How can wildlife biologists use metapopulation concepts to understand the processes that affect wildlife populations and to prescribe management approaches to preserving biodiversity? These are some of the questions addressed in *Metapopulations and Wildlife Conservation* edited by Dale R. McCullough. This timely and highly recommended volume is based on a symposium held at the first annual meeting of Wildlife Society in 1994. The symposium brought together some of the best theoretically and empirically based studies and models to summarize what has become one of the central themes in conservation biology, the identification, maintenance, and management of metapopulations. Readers will not be disappointed. The book starts off with five chapters that provide the theoretical basis and underpinnings for studying metapopulations. Dale McCullough introduces the metapopulation concept, provides working definitions, and argues convincingly that habitat loss and fragmentation are at the forefront of wildlife conservation. In chapter 2, Michael Gilpin provides an historical perspective on metapopulation analysis and models starting with Robert Levins' original paper in 1970 and showing how some of the more modern approaches incorporate patch size, quality, and connectivity to source-sink dynamics, animal movement, and gene flow. The genetics of metapopulations is amply covered by Philip Hedrick in which he demonstrates theoretically and quantitatively the relevance of maintaining heterozygosity, how to estimate effective population size, the significance of bottlenecks, and inbreeding depression. John Wiens provides a useful summary of habitat fragmentation in which he argues that habitat fragmentation is widely regarded as a—if not the—central issue in conservation biology. Wiens distinguishes between patches and islands, emphasizes the importance of scale, an animals' perception of fine- and coarse-grained habitats, patch isolation, and spatial configuration, corridors and connectivity, and the demographic consequences of maintaining habitat mosaics. William Lidicker and Walt Koenig argue that all edges are not the same and that an understanding of how edges are perceived and used by various groups of animals such as amphibians and reptiles, birds, and mammals needs to be considered in managing populations.

The following 11 chapters provide case histories for frogs (one chapter), birds (three chapters), and mammals (seven chapters). Each chapter is a summary and synthesis of previously published data, however, each is written comprehensively and provides sufficient information to get a clear understanding of the current status of the species. The methods are adequately presented, models are presented for most species, and management implications are made. The problems associated with various taxonomic groups become evident and a strong plea is made for understanding species-specific life history and demographic characteristics in management. For instance, dispersal capabilities, barriers to dispersal, distance between patches, and matrix habitats differ considerably for frogs (Per Sjorgren-Gulve and Chris Ray), spotted owls (Rocky Gutierrez and Susan Harrison), and grizzly bears (Lance Craighead and Ernest Vyse) and must be taken into consideration when developing management plans for maintaining metapopulations of these and other species.

Not surprisingly, some of the best data are provided for species that have been studied the longest, such as the Florida scrub jay (Bradley Smith, et al.). These authors show how the unique social system (cooperative breeding) and limited dispersal capability are incorporated into a population viability analysis which in turn is used to design a habitat preservation plan. Behavioral systems also play a role in space use, dispersal, colonization, and reserve design for kangaroo rats (Mary Price and Michael Gilpin), monk seals (John Harwood et al.), Steller sea lions (Anne York et al.), and cougars (Paul Beier). Readers will become frustrated at Beier's blow-by-blow account of his dealing with local bureaucrats and developers in

his plea to preserve and protect cougar habitat, but to little avail.

Some interesting conclusions that are developed in this summary of case histories is that although patterns of space use and response to fragmented habitats are founded in theory and follow certain predictions, many unique species-specific characteristics occur and must be considered in reserve design and conservation planning. For instance, mountain sheep are highly social and remain in maternal bands and are reluctant to colonize new habitats (Vernon Bleich et al.); Tule elk bottlenecked at less than five individuals in 1975 and have now grown to several thousand individuals distributed in 22 subpopulations, but with minimal genetic variation (Dale McCullough); spotted owl demography varies enough that the northern spotted owl fits a metapopulation model, whereas the California spotted owl fits an individual territorial model (Barry Noon and Kevin McKelvey); and a genetic analysis of grizzly bears suggests considerable gene flow among distant populations, even island populations (Craighead and Vyse).

All in all this is an excellent book. I used it for a graduate seminar course and the students thought it gave them an excellent introduction the theory, case histories, caveats, and conservation issues relative to spatially segregated populations. The chapters are easy to read and follow a central theme, yet show enough individuality to illustrate ordinal-, species- and behaviorally unique characteristics that need to be considered in conservation planning and managing wild populations. If any shortcomings exist in this book, they probably reflect the lack of knowledge in this area, a limitation that McCullough recognizes in the concluding chapter. For instance, we tend to fall into that proverbial trap of managing for species, rather than developing a community or ecosystem approach to management. How can we use the metapopulation concept to manage for species assemblages? Can case histories of some species be used as ecological model systems for other species? How do we identify (or even define) metapopulations? Are all populations metapopulations, and if so, what does the metapopulation concept teach us that we don't already know? All of these issues eventually need to be addressed and this book is an excellent place to start. In that our understanding of metapopulation dynamics is in its infancy, I await the sequel to this book five years from now to see how this field grows and matures in the succeeding years. This book is highly recommended for anyone working in population and conservation biology.

—Jerry O. Wolff's Graduate Seminar Class
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NORTHWEST SCIENCE

Information for Authors

Scope of Articles

The pages of *Northwest Science* are open to original and fundamental research in the basic, applied, and social sciences. *Northwest Science* does not publish notes or bibliographic papers. All submissions are refereed, usually by two reviewers. Papers are welcome from authors outside of the Pacific Northwest, but at least one author of any paper considered for publication must be a member of the Northwest Scientific Association.

Manuscripts

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The manuscript should consist of sections in the following sequence:

- Title Page
- Abstract
- Text (Introduction through Acknowledgments)
- Literature Cited
- Footnotes
- Tables
- Figure Legends
- Figures

Maximum article length for papers published in *Northwest Science* is 16 journal pages. Two typed pages are approximately equal to one journal page.

Numerals will be used to indicate footnotes unless such usage would be confused with numerical data. In this situation, lowercase letters should be used. Do not break, or hyphenate, words at the ends of lines. Words to be italicized should be typed in italics.

The format and style of manuscripts should conform to general usage in recent issues.

Title Page: The first page of the manuscript should contain:

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- Title of paper
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Abstract: The purpose of an abstract is to briefly summarize the study so it is quickly accessible to the general readership of the journal. The abstract, written in complete sentences and not exceeding 250 words, should precede the text on a separate page. Authors are reminded of the diverse disciplines and readership served by the journal. With this in mind the abstract should have three parts of unequal length. First, the abstract should begin with a statement of the purpose of the study that indicates *why the study was undertaken.* Next the experimental design or approach should be stated and the *results summarized.* The abstract should end with a sentence or two on the larger significance of the research. Authors are strongly encouraged to give the abstract proper attention.

Text: Literature citations within the manuscript text should contain the author's name and year of publication, using formats A and B.

- Format A:
  ...studied by Jones (1978)...
  ...studied by Smith and Brown (1979)...
  ...studied by Smith et al. (1980)... (if more than two authors in a citation)
- Format B:
  ...was previously investigated (Smith 1965, Jones 1971, Harris 1982)...

...results of other investigations (Smith 1966, 1970; Jones 1973; Brown 1974)...

Numbers from one to nine will be spelled out, while arabic numerals will be used for numbers 10 and larger. Exceptions to this rule are: 1) a series of "mixed" numbers (e.g., 14 elk, 35 deer, 2 bobcats, and 1 bear); 2) when the number immediately precedes an abbreviation for a standard unit of measure (e.g., 3 g, 18 mm, 300 m^2). Numerals will also be used for dates, times, page numbers, and percentages.

Present all data in international (SI) unites. English equivalents may be added parenthetically. Use the 24-hour clock (0600 and 2230) and continental dating (17 November 1986).

On first mention, a species should be designated by common name followed by systematic binomial (italicized). Common names for species should not be capitalized except when derived from a proper name. Thus, "mountain hemlock" or "white-crowned sparrow," but "Douglas-fir" or "Clark's nutcracker." For abbreviations and forms of titles for serial publications, follow the BIOSIS List of Serials. Consult with the Council of Biology Editors *CBE Style Manual,* 4th ed., for general information on manuscript preparation.

Literature Cited: Only the *first letter* of the *first word* of journal articles, technical reports, theses, etc. are capitalized. First letters of *major words* in book titles are capitalized. All authors of a title are listed in the bibliographic citation ("et al." is used only in the body of the text).

Citation of unpublished reports is discouraged. Rather, cite the sources as a personal communication from the senior author (P. W. Smith pers. comm.).

Citations should be double-spaced and listed in alphabetical order at the end of the article. Listed below are some typical citations.

Journal articles

Broadbooks, H. E. 1970a. Home range and territorial behavior of the yellow pine chipmunk *Eutamius amoenus.* J. Mammal. 51:310-326.

_____. 1970b. Populations of the yellow pine chipmunk, *Eutamius amoenus.* Amer. Midl. Nat. 83:472-488.

Ceska, A., and H. Romer. 1971. A computer program for identifying species group. Vegetatio 20:48-73.

Grizze, J. E., C. F. Starmer, and G. G. Kuch. 1969. Analysis of categorical data by linear models. Biometrics 25:489-504.

Monographs or books

Jennings, H. S. 1906. Behavior of the Lower Organisms. Columbia University Press, New York.

Papers in proceedings or symposia

Ryland, J. S. 1975. Parameters of the lophophore in relation to population structure in a bryozoan community. *In* H. Barnes (ed.) Proc. 9th Eur. Mar. Biol. Symp., Aberdeen University Press, Aberdeen. Pp. 363-393.

Theses, dissertations, personal communications, and articles in press

Donald, D. B. 1971. The limnology of the plankton of three temporary pons in Alberta. University of Calgary, Calgary. M.S. Thesis.

Wiser, H. C. 1961. Decomposition and homogeneity of continua on 2-manifolds. University of Utah, Salt Lake City. Ph.D. Dissertation.

Danwiddie, P. W. In Press. Dichotomous key to conifer foliage in the Pacific Northwest. Northw. Sci.

Technical Bulletins

Daubenmire, R., and J. B. Daubenmire. 1968. Forest vegetation of eastern Washington and northern Idaho. Wash. Agric. Exp. Sta. Tech. Bull. 60. Washington State University. 210 p.

Goodwin, J. G., Jr., and C. R. Hungerford. 1979. Rodent population densities in pine forests. USDA For. Serv. Res. Pap. RM-214. Rocky Mtn. For. Range Exp. Sta., Fort Collins, Colorado. 39 p.

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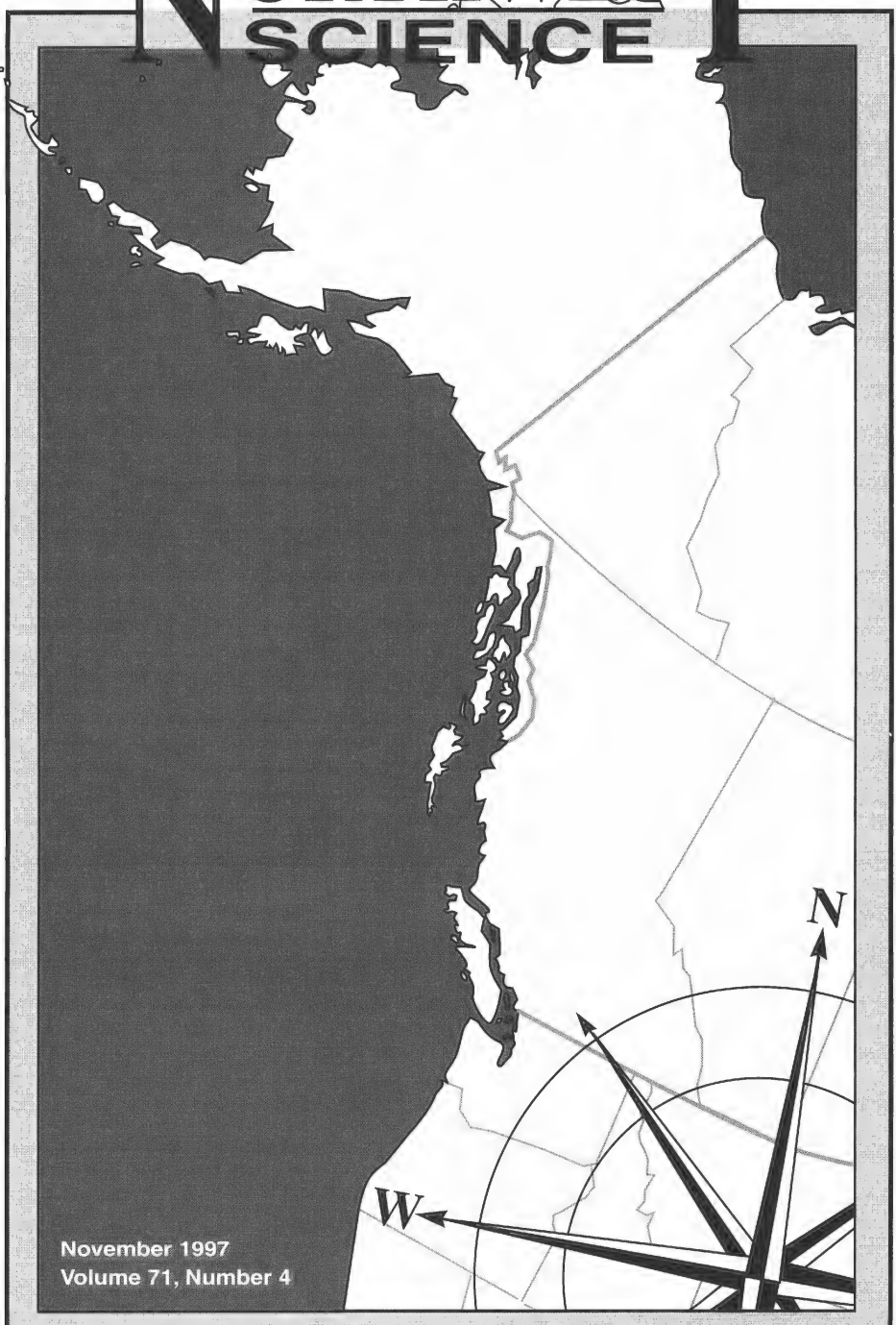
NORTHWEST SCIENCE



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Announcements

1998 Annual Meeting, The Evergreen State College, March 25-27

The 71st annual meeting of the Northwest Scientific Association will be hosted by The Evergreen State College at its campus near Olympia, Washington. The meetings will be held jointly with the Society for Northwestern Vertebrate Biology and the Lichen Guild on March 25-27, 1998. Following a business meeting of the Governing board on March 25, scientific sessions will occur on the following two days with a variety of concurrent sessions and symposia. Work is underway for symposia on rare plants, the USFS's DEMO project, and forest canopies. An opening plenary symposium on the interface between scientific research and governmental policy is under consideration. Field trips to ecological research sites on Fort Lewis, Northwes Trek Wildlife Park, and the canopy crane site are also being planned.

Members of all the sponsoring groups as well as nonmembers are welcome at the meetings, and students are especially encouraged to attend and report the results of their research at the meeting. The call for abstracts and registration information has been mailed to all members of the Association.

Information about the meeting may be obtained from Richard Cellarius, meeting chair, or Gabe Tucker, program chair, at The Evergreen State College, Olympia, WA 98505; e-mail address is nwsa@elwha.evergreen.edu. The address for accessing meeting information on the World Wide Web is http://www.evergreen.edu/nwsa98.

1998 Student Research Grants

Student research grants are available to be awarded. Applicants must be student members of the Northwest Scientific Association at the time they submit their proposal (see inside front cover for information about joining the society).

Preparation of the Proposal

A cover page should be provided that includes:

- title of proposal
- name and address (including phone number and e-mail) of applicant and associated institution
- name of major professor/advisor
- amount of money requested (maximum $500)

The proposal should include:

- title
- statement of justification (purpose, objectives, and hypotheses)
- methodology/experimental design (including methods of analysis)
- detailed budget; no salaries (on separate page)

The text of the proposal should be **no more than three (3)** double-spaced (12-pt font) pages (not including the title, literature cited, and budget pages).

(Continued, next page)

Four copies of the proposal are due **on or before February 5, 1998;** send to:

Dr. Jerry O. Wolff
Department of Fisheries and Wildlife
Nash 104/Oregon State University
Corvallis, OR 97331 Phone 541-737-2473 Email: wolffj@ccmail.orst.edu

Grant winners will be announced at the annual meeting of the Northwest Scientific Association held at Evergreen State University, Olympia, Washington, March 25-27, 1998.

Awards provided by the Northwest Scientific Association are designed to help students complete research projects in the basic and applied sciences. Monies should be used only to support research activies of the student. Grant support **can not** be used for salaries. Students will be expected to present the results of their research at a future NSA meeting.

Geoffrey G. Parker, Smithsonian Environmental Research Center, P.O. Box 28, Edgewater, Maryland 21037

Canopy Structure and Light Environment of an Old-growth Douglas-fir/ Western Hemlock Forest

Abstract

The three-dimensional light environment within the canopy of a tall coniferous forest was sampled to quantify its variation and localize the sites of radiation absorption. Broadband visible (PAR) and ultraviolet radiation (UVB) were measured around midday in midsummer in an old-growth Douglas-fir/Western Hemlock forest in the Cascade Range in southern Washington using sensors suspended from the gondola of a large tower crane. Patterns of vertical transmittance varied greatly between locations and showed abrupt transitions from bright to dark conditions at varying heights. The average light field in this canopy with trees to 60 m was resolved into three functional zones. Above 40 m from the ground is a "bright zone," where light was reliably intense and predominantly in the direct beam component, and below 12 m, a "dim zone," where light was reliably low and mostly diffuse. Between these levels is a "transition zone," with a steep vertical gradient in light transmittance, high horizontal variation, and a mixture of beam and diffuse components. The pattern of UVB light was very similar to that of PAR. From the general transmittance profile the vertical structure of the canopy was estimated to have a peak density of foliage at 12 m (less than one quarter of the stand height) with declining densities above and below. The "bottom-heavy" canopy structure found in this study differs markedly from the "top-heavy" profiles reported from managed or young stands.

Introduction

Vegetation canopies influence the intensity, quality and distribution of radiation. The production of dry matter in forests is closely related to the amount of visible light absorbed in the canopy (Monteith 1977, Linder 1985, Cannell et al. 1987, Monteith 1994), which is related to the three-dimensional organization of canopy elements (e.g., Monsi et al. 1973, Jarvis and Leverenz 1983, Norman and Campbell 1989). Often, aspects of canopy structure are inferred from measurements of canopy light. However, estimation of whole-canopy structure requires information on light on the scale of the whole canopy. Yet studies of forest light environments are usually limited to observations from fixed structures (such as towers) or from the ground (e.g., Pierce and Running 1988, Parker 1995) and can rarely yield patterns representative of the whole canopy. Thus there is little understanding of the general attenuation of light with depth in the canopy, of the point-to-point variation in within-canopy light, or of the relation between canopy structure and light environment in three dimensions.

Stand-level measurements of variation in light within the canopy are uncommon. Most attempts to account for variation have been made over limited ranges, such as within the reach of a tower (e.g., Acock et al. 1969, Thompson and Hinckley 1977, Ellsworth and Reich 1993, Vose et al. 1995) or an individual large tree (Yoda 1978). Suitably extensive observations have been obtained using balloon-mounted sensors (Parker et al. 1996). However, wind shear often makes it difficult to acquire measurements near the top of the canopy. In principle, a tall construction crane could provide the horizontal coverage and stability for truly three-dimensional radiation measurements (Parker et al. 1992) but this application has not been reported.

The objectives of this study were to: 1) assess the suitability of a tower crane system for obtaining light measurements within the canopy of a tall old-growth conifer forest; 2) quantify the vertical pattern of attenuation and the spatial variation of the radiation field; and, 3) infer some aspects of average canopy structure from such radiation measurements.

Materials and Methods

Vertical transects of within-canopy light measurements were obtained 27 and 28 July 1995, within the circle of the tower crane of the Wind River Canopy Crane Research Facility (WRCCRF). The stand is an old-growth Douglas-fir/Western Hemlock forest in the Thornton T. Munger Research Natural Area of the Gifford Pinchot National Forest (Wind River Ranger District) in the Cascade range of southern Washington (45°49'N, 121°58'W). The site, near the upper limits of the western

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hemlock zone (Franklin and Dyrness 1973), is relatively flat - the elevation range within the crane circle is 6 m (D. Shaw, personal communication). The stand is about 400-500 years old (Franklin and DeBell 1988) with a Douglas-fir (*Pseudotsuga menziesii*) overstory (to 60 m), a western hemlock (*Tsuga heterophylla*) midcanopy and an understory of Pacific silver fir (*Abies amabilis*) and Pacific yew (*Taxus brevifolia)* (DeBell and Franklin 1987).

A Liebherr 550 HC tower crane (Morrow Crane Inc., Salem OR) was used to access the canopy (Holden 1995). The crane center is about 550 m north into the stand along forest road N400. The jib of the crane stands 74.5 m above the tower base and has a range of 85 m, providing access to 2.3 ha of the stand. A suspended personnel platform ("gondola") allowed virtually unrestricted access to any point in the canopy space.

Two radiation sensors were attached to a 15 x 30 cm plexiglass platform suspended 10 m below the rail of the crane gondola. The sensors included a quantum sensor (model LI-190 SB; Li-Cor, Inc., Lincoln NB) which yielded photosynthetic quantum flux (PAR, in $\mu mol\ m^{-2}s^{-1}$) and a Robertson-Berger type UVB meter (model 2D; Solar Light, Inc., Philadelphia PA), which gave biologically-effective UV dosage (UVB, in minimal erythemal doses hr^{-1} [see Berger 1976]). Cables from the sensors led to the gondola where readings were noted from the appropriate display. The sensor platform could be inverted to yield measurements of upwelling light. The platform was leveled with a bull's eye level before and after each transect. In all, 16 vertical transects were made of downwelling light; at four of these locations, transects of upwelling light were also made. Figure 1 shows the transect locations relative to

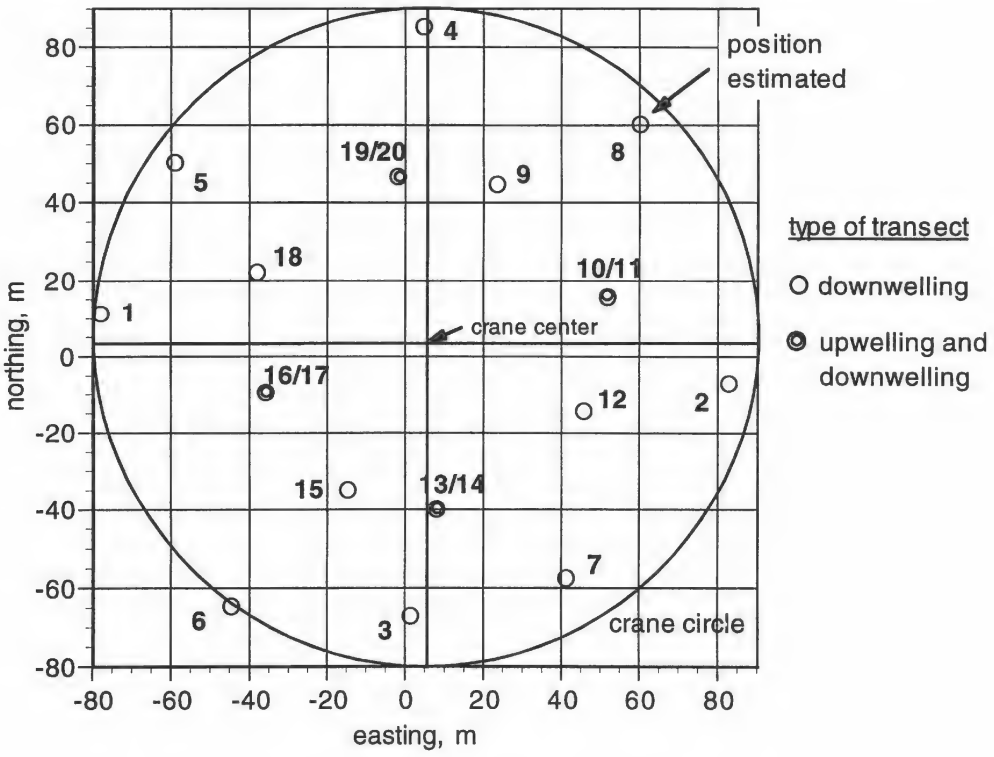

Figure 1. Sixteen locations within the WRCCRF crane circle used for measurements of radiation in vertical transects. Twelve were used for downwelling light only and four for both upwelling and downwelling light. The numbers identify the individual transects.

the coordinate system of the site stem map (see http://cqs.washington.edu/people/eliz/sitemap.html). Most of the transects were in gaps of different sizes; relative sizes of these openings were noted.

To avoid damage to the crane hoisting motor with repeated stopping and starting, measurements were taken at regular intervals during a continuous hoist from the ground to maximum height. Hoisting in "clutch 2, step 2" gave a reliably constant vertical velocity (ranging 0.18 - 0.20 m s^{-1}). Measurements were taken every 10 seconds; the vertical position calculated from time and velocity gave a mean resolution of about 1.9 m. Height above ground was noted and depth below a reference plane (including a correction for the deflection of the jib when loaded by a gondola and three people) was calculated for each measurement.

Measurements were taken within 2.5 hr of solar noon (range 1147-1528 PDT). These corresponded to a mean sun elevation angle of $60.5 \pm 3.4°$ (range 51.7-63.5). PAR and UVB values were all converted to fractions of the maximum above-canopy values for each transect. This ratio is called transmittance here.

Layer Budget of Radiation Components

To obtain mean profiles, the data were grouped by 2 m height intervals (centered on even heights) and statistics for both upwelling (sensors pointed down) and downwelling (sensors pointed up) measurements and both wavebands were calculated. The components of the radiation budget (absorbance [A], transmittance [T], and reflectance [R]) for each canopy layer between measurement levels were then estimated:

$$A[n+1,n] = D_{n+1} - D_n + U_n - U_{n+1},$$
$$T[n+1,n] = D_n + U_{n+1}, \text{ and,}$$
$$R[n+1,n] \approx U_{n+1} - U_n,$$

where the U and D denote the measured upwelling and downwelling components of either PAR or UVB from level n to level n+1; n increases with height from the ground. For each waveband these values were in turn scaled by the maximum D_{n+1} at the top of each transect.

Vertical Foliage Distribution

To estimate the vertical distribution of radiation-occluding material (assumed to be foliage mostly), the mean vertical pattern of PAR attenuation and the general relationship describing light attenuation in turbid media, the Beer-Lambert (B-L) law, was used. Because the absolute leaf area index (LAI) of the study stand was not available, the estimation focused on the relative profile, the fraction of the cumulative downward LAI at a given canopy depth.

First, the normalized extinction coefficient, k_r (the subscript r denotes a normalized variable), was estimated by inverting the B-L law:

$$k_r = - \frac{\ln(I(z)/I(0))}{L_r(z)},$$

where I(0) and I(z) are the radiation flux at the top of the canopy and at depth z, respectively. $L_r(z)$ is the normalized profile, i.e., the fraction of all PAR-absorbing area from the top of the canopy (z=0) to depth z. At the bottom of the canopy, $L_r(z)$ equals 1. Whereas the usual k is the logarithm of the fractional reduction in light per unit area, k_r is normalized over all the absorbing area (k_r is the product of k and LAI). As shown later, the mean penetration of PAR at the forest floor was about 0.05, yielding a bulk k_r of ≈ 3.0 (because $k_r = \ln(I(z)/I(0))$ when $L_r(z) = 1$). Using this value, $L_r(z)$ was calculated from the normalized B-L relation,

$$L_r(z) = - \frac{\ln(I(z)/I(0))}{k_r},$$

where I(z)/I(0) is the mean penetration at depth z. The profile of I(z)/I(0) was smoothed with a 4-point moving average. Finally, the fraction of absorbing area at each level z was extracted from the downward cumulative $L_r(z)$.

Results

Transmittance profiles of PAR (Figure 2) varied greatly among locations. In most of the profiles, there were abrupt transitions from nearly full sunlight to very dark conditions. There was little evidence of the gradual diminution of radiation intensity with depth reported from profiles in other stands (Yoda 1978, Parker et al. 1995). The height above ground where light changed swiftly (the "lumicline") varied greatly among transects. The height of the lumiclines (where the transmittance profile first declines below half of the incident flux) varied from about 12 m (transect 9) to 36 m

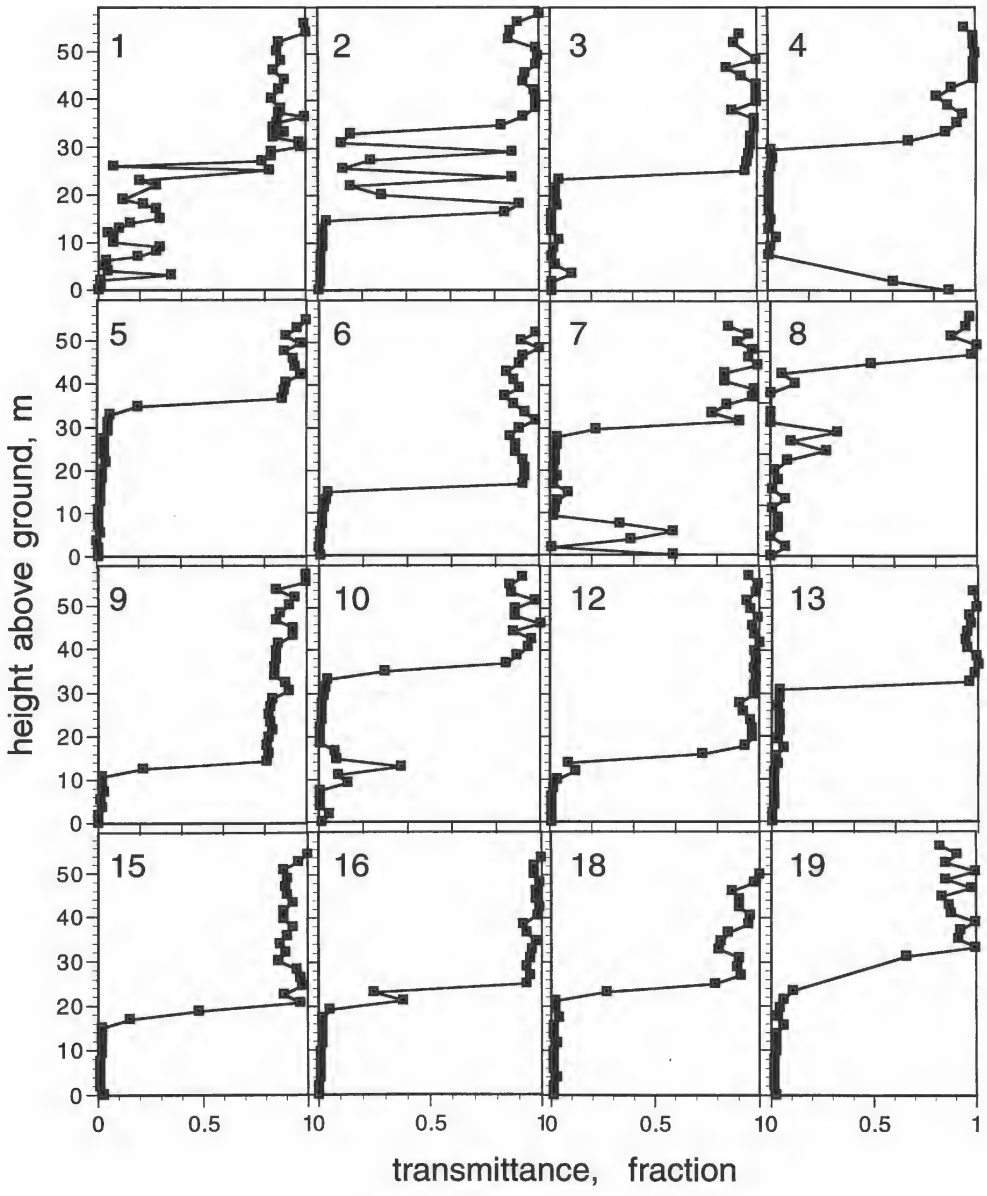

Figure 2. Variation in PAR transmittance profiles. The numbers identify each downwelling light transect in sequence. Transects 1, 6, and 15 were in large gaps; 2, 5, 12, 16, 19 in medium-sized gaps; 9 and 13 in small-medium gaps; 3, 4, 7, and 18 in small gaps; number 10 was in a very small gap.

(transects 5 and 10). The vertical patterns for UVB transmittance were similar to those of PAR.

The pattern of illumination in individual profiles was generally consistent with the size of the canopy opening: big gaps had lower lumiclines and deeper penetration of bright light than did small ones (Figure 2). However, not all transects conformed to this rule - transect 1 was in a large gap with a high lumicline and transect 4 was in a small gap but had a low lumicline.

The general vertical patterns of mean PAR flux and its variability are illustrated in Figure 3a. Transmittance near the forest floor averaged about 5%, though at the very bottom there was an increase in light. Note that, at any canopy level, almost any flux was possible, even relatively high transmittances near the forest floor (e.g., transect 4 in Figure 2). This general pattern was also apparent for UVB (Figure 4a). The mean upwelling light in both bands also diminished with canopy depth. However, in contrast to the curved mean pattern for downwelling light, upwelling light had a nearly linear decline with depth. The reflectances implied by these measurements were very low in both wavebands (maximum of <1% for UVB and <3% for PAR).

The horizontal variation in transmittances, as estimated by the standard deviation of observations at a given height, was low in the upper canopy and in the deepest layers of the forest, but high in the midcanopy (Figures 3b and 4b). Thus, PAR and UVB are the least predictable where they change most rapidly. The relative variability, estimated by the coefficient of variation (standard deviation/mean) was very low in the outer canopy and grew steadily greater with depth in the canopy, to more than 200% near the forest floor. PAR showed more variability at almost all layers than did UVB (Figure 5). The patterns in spatial variation in upwelling measurements were similar to those of the downwelling portion.

The components of the layer budget of radiation (Figure 6) illustrated that reflectance was nearly zero in all layers, and that absorbance was most

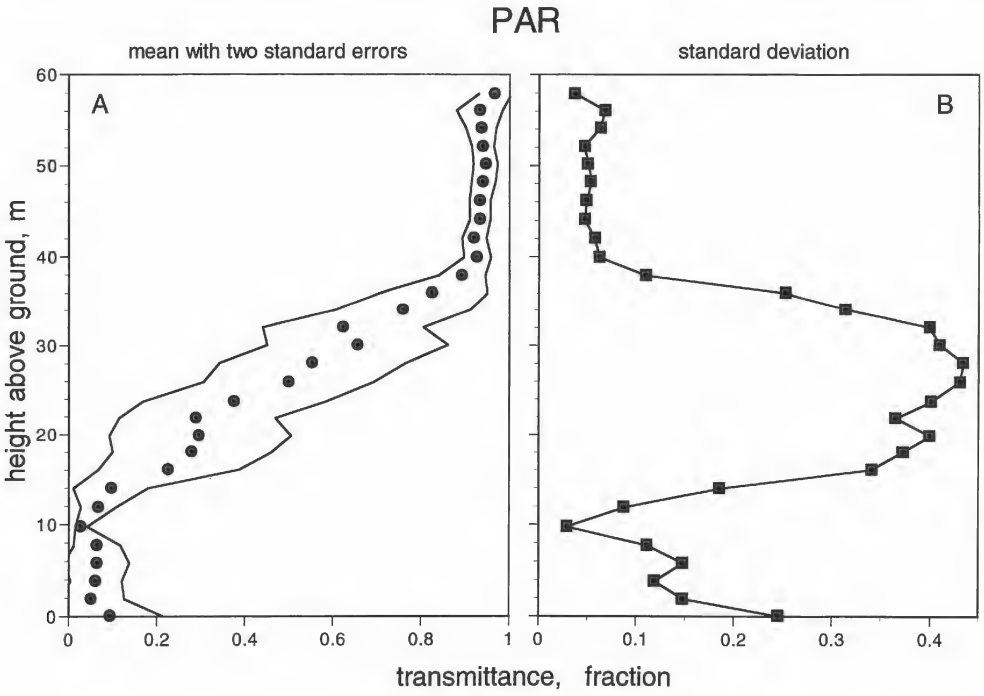

Figure 3. The profile of mean PAR transmittance with two standard error bounds (A) and of the spatial variability of PAR transmittance with height, indicated by the standard deviation (B).

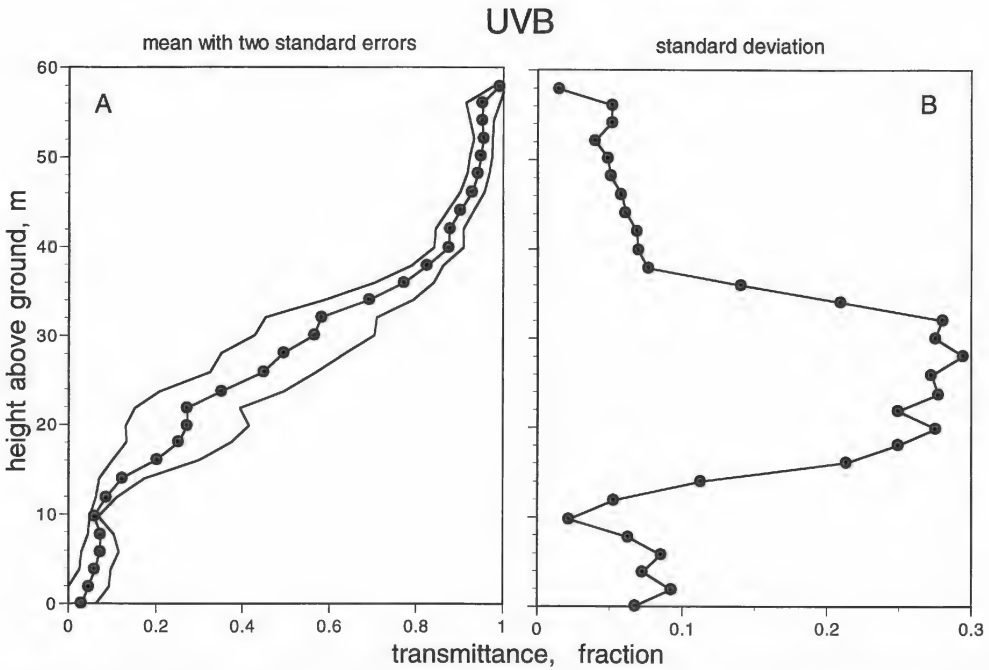

Figure 4. The profile of mean UVB transmittance with two standard error bounds (A) and of the spatial variability of UVB transmittance with height, indicated by the standard deviation (B).

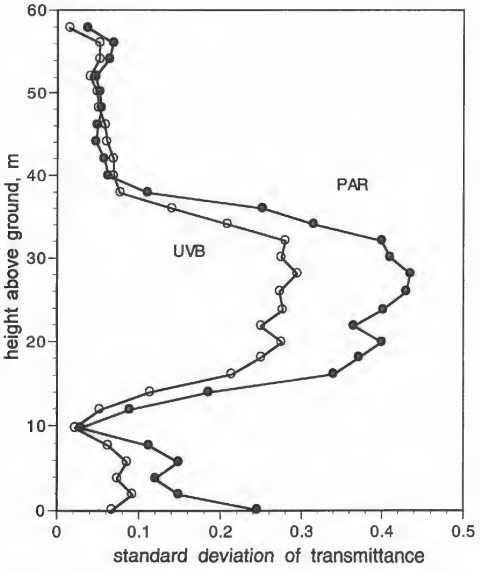

Figure 5. Spatial variation of vertical transmittance compared between the PAR (filled circles) and UVB (open circles) wavebands.

pronounced in the layers of greatest change in transmittance (between 14 and 40 m). The separation into these components is very similar for the PAR and UVB bands.

The inferred vertical distribution of PAR-absorbing material (including foliage, epiphytes, cones, branches, and stems) has a prominent mode between 9-15 m. Above this point to nearly 50 m, a gradual decline with height occurs and below, a rapid decline in PAR-absorbing material was noted (Figure 7b). The level adjacent to the forest floor had little effect on light attenuation. The median height of PAR-absorbing material in this stand is at about 16 m (Figure 7a).

Discussion

Measurements were taken only under the clearest conditions; observations that were obviously influenced by clouds or the shadow of the crane jib were deleted. However, occasional wispy clouds and haziness could have diminished the values of incident light and affected the calculation of transmittances. The small effect of such cloudiness

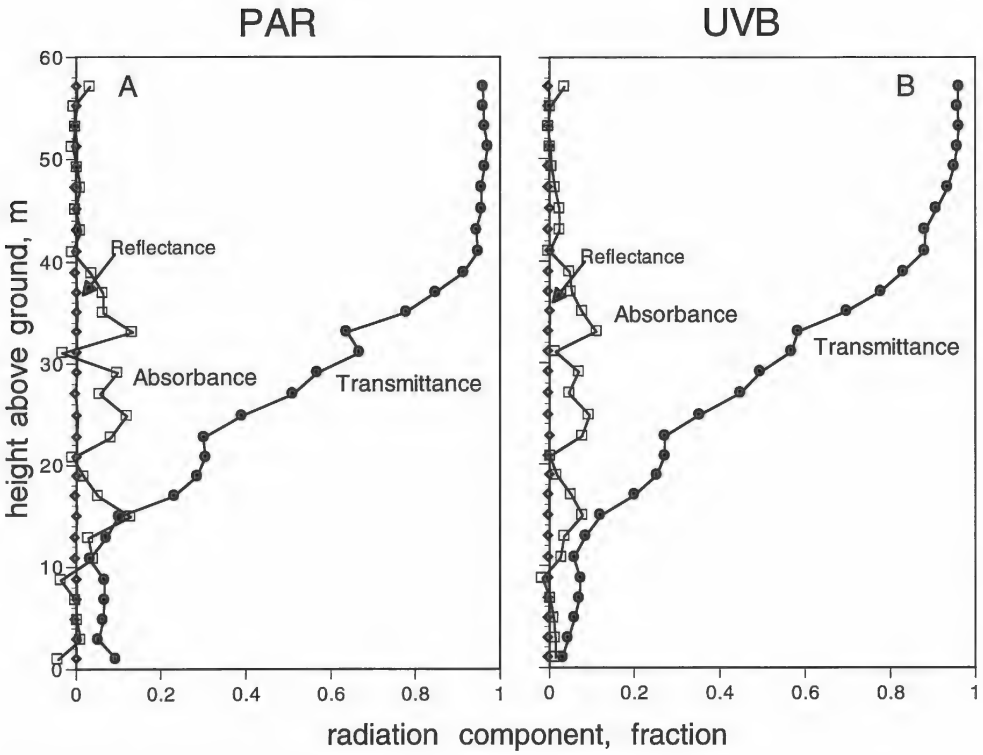

Figure 6. The estimated radiation budget for each 2m layer of the canopy, as defined in the text, for the absorbance, transmittance, and reflectance components for PAR (A) and UVB (B).

is suggested by the variability in transmittance at heights above the canopy (Figure 2).

Observations were taken in openings between crowns where the sensor platform could be inserted. Many, but not all, were gaps caused by the death of overstory trees. It was not possible to sample in the near-bole region with the sensor platform. This restriction to more open areas means that the profiles presented are biased to the brighter regions of this canopy. The mean profile is likely somewhat brighter than would be found in an unrestricted survey.

The calculation of the layer radiation balances assumes that the upwelling and downwelling measurements account for all the light exchanges with a given layer, that lateral light is negligible at this scale. However, mean transmittances can sometimes increase with depth (e.g., in this study the forest floor was brighter in PAR than the level just above it). It is more likely that the reverses in the mean profile reflect inadequate sampling, since an additional source of light is questionable in extensive forests. With more samples the mean transmittance pattern would likely become monotonic. However, since upwelling fluxes were very small, the separation of radiation components is apparent from the transmittance profile: transmittance is mostly the light downwelling from a layer; absorbance is essentially the change in downwelling light; and, reflectance is negligible.

Three distinct functional zones of radiation may be recognized in this stand by considering the vertical pattern of the mean and variability of transmittance of both wavebands (Figure 8). In the outer canopy, more than 40 m above the ground, is a zone of consistently bright light (the "bright zone") and in the lower canopy, below 12 m, is a zone of reliably dark conditions (the "dim zone"). Between these limits is a region where the mean light levels diminish rapidly with depth, with

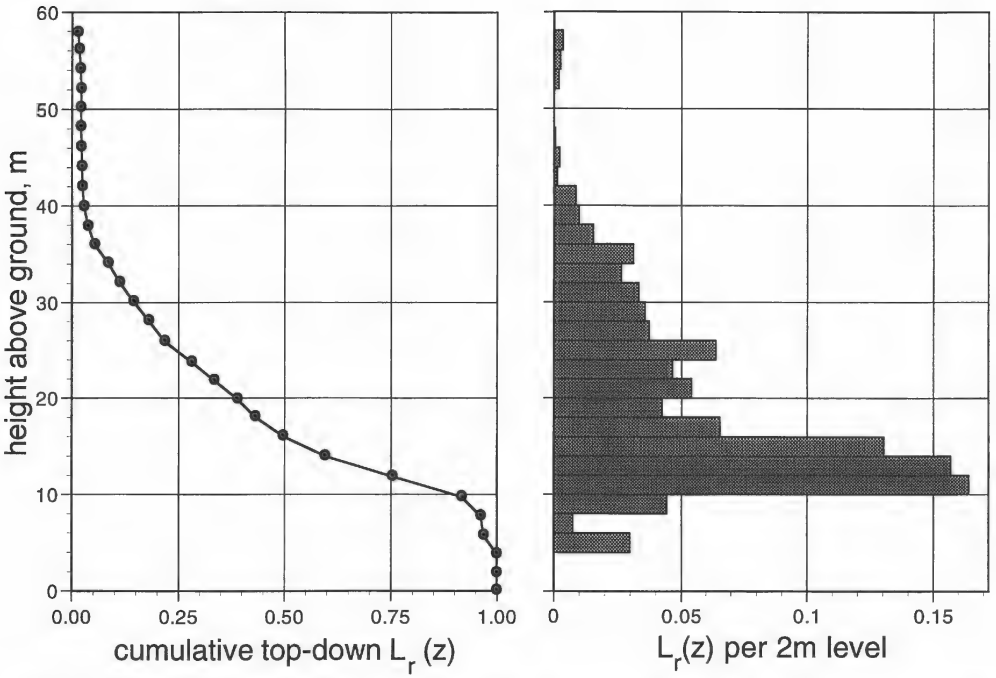

Figure 7. The vertical profile of relative leaf area ($L_r(z)$), as inferred from the bulk absorbance, the normalized extinction coefficient (k_r), and the mean profile of transmittance. The left panel (A) gives the cumulative downward $L_r(z)$; the right (B) gives $L_r(z)$ by 2m layer.

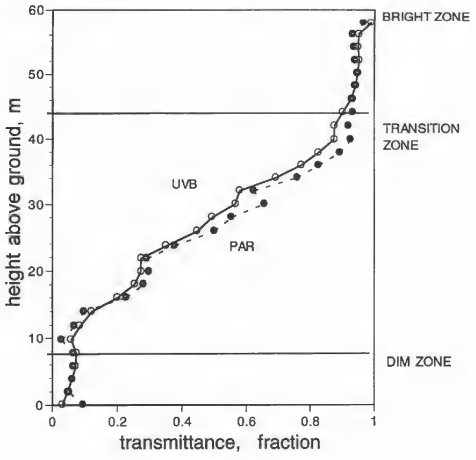

Figure 8. A proposed organization of the canopy light environment at the WRCCRF based on the average and variability in the vertical transmittance of PAR and UVB radiation.

extremely high horizontal variation (the "transition zone"). The abrupt transitions from bright light to deep shade (the lumicline), suggest that the transition zone (Figure 8) is where two extreme light regimes (bright and dim) are mixed in varying proportions. Light in the bright zone is mostly direct and, in the dim zone, predominantly diffuse; light in the transition zone is a mixture of these. The limits of these zones probably vary over daily and annual cycles but those given are probably applicable when the sun is highest above the horizon and radiation income is greatest. At least one-fifth of the annual light input at this latitude is received in the range of sun angles observed in this study.

It is surprising that the mean pattern of transmittance is so smooth, given the abrupt shapes of the individual profiles, the small number of profiles averaged, and the structural heterogeneity of the stand. Because the lumicline is not a feature of the mean light environment, an individual

transmittance profile in this stand is likely not to be representative of the average. The shape of profiles in the WRCCRF canopy differs from patterns reported in other, non-coniferous forests where individual profiles are often smoother (e.g., Yoda 1978, Parker et al. 1996). The abrupt transitions from light to dark along the vertical transects are a consequence of moving into the shade of individual crowns. Conical-crowned trees with needle-leaf foliage can have a very high foliage density and be efficient absorbers of lateral light.

The pattern of UVB radiation was smoother in vertical attenuation, with less spatial variation in both upwelling and downwelling components than was the pattern for PAR. This is consistent with Brown et al. (1994) who found UVB varied less abruptly in space than PAR in a variety of forest light environments, probably because UVB derives from diffuse (sky) radiation and not primarily from the direct beam of the sun (as for PAR).

The inference of vertical structure from the pattern of radiation relies on several assumptions. It requires a monotonic transmittance profile (for small data sets, where increases in light with depth could be observed, smoothing might be necessary). It also assumes that the extinction coefficient inferred from ground-level transmittance (the bulk extinction coefficient) may be applied throughout the canopy. However, such a lumped descriptor may not apply where the foliage characteristics (tissue makeup, species composition, orientation angles, clumping) are not average. This problem applies whether using a conventional extinction coefficient (k) or the normalized version (k_r) presented here. Note also that since the sampling was somewhat biased to brighter canopy regions, the vertical distribution of PAR-absorbing surfaces will be shifted to higher elevations than is estimated here (Figure 7). The extent of this shift is probably small.

It has been assumed that most of the radiation absorption was by foliage, however this was not determined in this study. Other sorts of canopy components (epiphytes of various sorts, reproductive tissues, twigs, branches, and stems) undoubtedly absorb some light. But foliage probably dominates absorption: it has the greatest area of canopy components and is positioned to intercept light. However, until direct measurements of L(z) are available, the relative profile ($L_r(z)$) provided by the normalizing method can serve as a hypothesis on the mean vertical structure of the WRCCRF canopy.

The proposed vertical structure is consistent with that expected for a collection of conical crowns having a smooth and declining diameter distribution. The height of the maximum, however, depends on the distribution of PAR-absorbing area within crowns. By aggregating idealized crowns van Pelt and North (1996) estimated the vertical distribution of crown volume in this stand had a single peak at 30 m above ground. The disparity between their estimate of the height of canopy maximum and that of the present study ($\approx$ 12 m) is probably because the density of PAR-absorbing material is not constant within a volume of crown.

The canopy structure inferred in this work differs from others reported for old-growth or conifer forests: the distribution of PAR-absorbing material has a maximum at a relatively low height above ground - around one quarter of the total canopy height - a "bottom-heavy" canopy distribution. In the more commonly reported pattern the majority of canopy area is nearer the top ("top-heavy" structure). However, the novelty of this finding may reflect the choice of stands usually studied: many canopy studies intentionally focus on stands of simple structure (such as conifer plantations) which almost always have top-heavy canopy structure (e.g., Stephens 1969, Ford and Newbould 1971, Kellomäki and Oker-Blom 1983). Older forests examined for canopy structure have been broad-leaved stands, where the vertical structure may be even (e.g., Aber 1979, Brown and Parker 1994) or complex (Parker 1995). Additional observations of canopy structure are needed in older, non-plantation, conifer forests.

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Genetic Diversity in the Introduced Clonal Grass *Poa bulbosa* (Bulbous Bluegrass)

Abstract

Bulbous bluegrass (*Poa bulbosa*) is a perennial bunchgrass with a widespread distribution throughout its native range in Europe and the Mediterranean. This grass has been introduced into North America and now occurs throughout much of the western United States. Within its native range, bulbous bluegrass reproduces mainly through sexual means; however, in North America clonal reproduction occurs primarily through the production of vegetative structures called bulblets. High chromosome counts are frequently reported for this species and suggest it is a polyploid. To assess the level and pattern of genetic diversity of bulbous bluegrass across a portion of its introduced range, a total of 10 populations from Idaho, Oregon, and Washington were analyzed by staining for 14 enzymes that were coded for by 19 genetic loci. Results indicate that bulbous bluegrass contains higher levels of genetic variation than expected for an introduced clonal plant species: 27.9% of loci are polymorphic per population, with an average of 1.54 alleles per locus, and a mean observed heterozygosity of 0.202. On average, 64% of all individuals within these populations possess three or four alleles at one or more loci; a value consistent with previous reports for autopolyploid species. A total of 84 multilocus genotypes were detected in these 10 populations, with an average of 9.6 genotypes per population. The number and complex distribution of multilocus genotypes observed in this study may be the result of multiple introductions of this species into its new range, and/or occasional sexual reproduction within introduced populations.

Introduction

Biological invasions are defined as the successful introduction and establishment of an organism into a region or habitat that was previously unoccupied by that species (Mack 1985). Biological invasions can vary geographically from simple range extensions to intercontinental migration (Barrett and Richardson 1986). Successful invaders (whether they be plants or animals) often possess the ability to aggressively colonize a new territory, with rapid range expansion across the introduced region (Mack 1985, Barrett and Richardson 1986, Barrett and Shore 1989). Once invasions occur, they can pose ongoing problems because they can act as vectors for disease, be expensive, alter ecosystem processes, and reduce biological diversity (Vitousek et al. 1996). In addition, several recent reviews have focused on the issue of biological invasions as forces for global change (D'Antonio and Vitousek 1992, Vitousek et al. 1996). Additionally, invasive species provide biologists with excellent model systems for genetic and evolutionary studies (Baker and Stebbins 1965, Barrett and Husband 1990). Invasive plant species are commonly reported to possess uniparental reproductive systems, be polyploids, contain depauperate levels of genetic variation within populations, have high levels of genetic differentiation, and exhibit multilocus structure among introduced populations (Baker 1974, Brown and Marshall 1981, Barrett and Richardson 1986).

Traditionally, introduced populations are believed to be established by only a small number of immigrants, often resulting in a loss of genetic variation through sampling effects (Barrett and Richardson 1986, Barrett and Shore 1989). In addition to founder effects and genetic bottlenecks, an absence of repeated immigration events will contribute to high levels of genetic differentiation among populations (Brown and Marshall 1981, Wade and McCauley 1988). Conversely, multiple introductions of different genotypes at the same or nearby locations can result in greater genetic variation in founder populations (Barrett and Husband 1990). Recent genetic evidence for cheatgrass (*Bromus tectorum* L.) and white bryony (*Bryonia alba* L.) suggests that multiple introductions of alien species may be more common than previously thought (Novak et al. 1991, Novak and Mack 1993, Novak et al. 1993, Novak and Mack 1995).

Uniparental reproductive systems, such as self-pollination or clonal reproduction (i.e. agamospermy and vegetative propagation), can be a beneficial characteristic for immigrants, and are

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common among species regarded as highly successful colonizers (Stebbins 1957, Brown and Marshall 1981). Selfing and clonally reproducing species are capable of producing progeny without the presence of a mate which, 1) frees them from the dependency of pollinators, 2) ensures reproductive success despite unfavorable conditions, 3) preserves adaptive gene complexes for all individuals within the population, and 4) allows a single individual to start an entire colony or invasion (Stebbins 1957, Williams 1975, Barrett and Richardson 1986). With clonal reproduction, progeny will be identical to their parents, and therefore, some models suggest that clonally reproducing species possess little or no genotypic variation within populations (Williams 1975). However, a second group of models claim that the level of genetic diversity in clonal species can, in fact, be similar to sexual ones (Maynard Smith 1971, Lynch 1984, Ellstrand and Roose 1987). This study examines the level and structure of genetic diversity in the clonally reproducing introduced plant species bulbous bluegrass (*Poa bulbosa* L.) (Poaceae).

Study Species

Bulbous bluegrass displays many of the ecological characteristics of a successful invasive plant species. This perennial bunchgrass is widespread throughout western Europe and the Mediterranean region (Cronquist et al. 1977), and is more rarely distributed in southern and eastern Britain (Humphries 1979). It is commonly found within pastures, roadsides, and other disturbed areas at low to middle elevations (Cronquist et al. 1977). Bulbous bluegrass was introduced in the eastern United States in 1906 (probably from Russia), and it was introduced in the western United Sates in 1915 as a contaminant in alfalfa seed (Harrison et al. 1996). Following its introduction in the West, this grass quickly spread throughout much of the Intermountain West because it is aggressive, highly competitive, persistent, and can become a dominant species in heavily disturbed (overgrazed) habitats (Harrison et al. 1996). In addition, rapid range expansion of bulbous bluegrass was facilitated by the purposeful introduction of the grass to prevent soil erosion or control more troublesome weeds (Younger and McKell 1972). Samples have been collected in New York, North Carolina, Virginia, North Dakota, Oklahoma, and most western states including California, Oregon, Washington, Idaho, Montana, Wyoming, Utah and Colorado (Hitchcock 1971).

Although bulbous bluegrass chiefly reproduces through sexual means within its native range, it is primarily an asexually reproducing species within North America where clonal production of propagules, or bulblets, have replaced the production of seeds (Hitchcock 1971, Younger and McKell 1972, Cronquist et al. 1977). Also, bulbous bluegrass possesses several bulbous bases, where each base is capable of giving rise to a new plant if detached and dispersed (Humphries 1979). Although high chromosome counts have been reported for bulbous bluegrass ($2n = 28, 35, 42$), suggesting that it is a polyploid, the literature does not indicate the type of polyploidy that occurs within this species (Cronquist et al. 1977).

Investigating the population genetics of an invading species may provide insights into the nature of its introduction into its new range. With this paper, we report results from our analysis of 10 populations of bulbous bluegrass from Idaho, Washington, and Oregon. The specific objectives of this study were to: 1) determine the level and structure of genetic variation within and among populations using enzyme electrophoresis, 2) assess the pattern of genetic variation and determine if they provide insights into introduction dynamics (single or multiple introductions events), 3) compare the results obtained for bulbous bluegrass to other studies of introduced and clonally reproducing plant species, and 4) and determine the genetic consequences of polyploidy for this species (i.e., type of polyploidy).

Materials and Methods

Plant Collections

As a first effort to describe the genetic variability of bulbous bluegrass, ten local populations were collected from various locations in Idaho, Oregon, and Washington (Figure 1, Table 1). Population collections were made between June and August, 1996, typically in disturbed habitats such as vacant lots and along roadsides. In addition, these populations also varied in their size and density (Table 1). The panicles of thirty to forty separate individuals in each population were collected at regular intervals (approximately 1 m) while walking through the population and stored within separate envelopes. Panicles were harvested when they

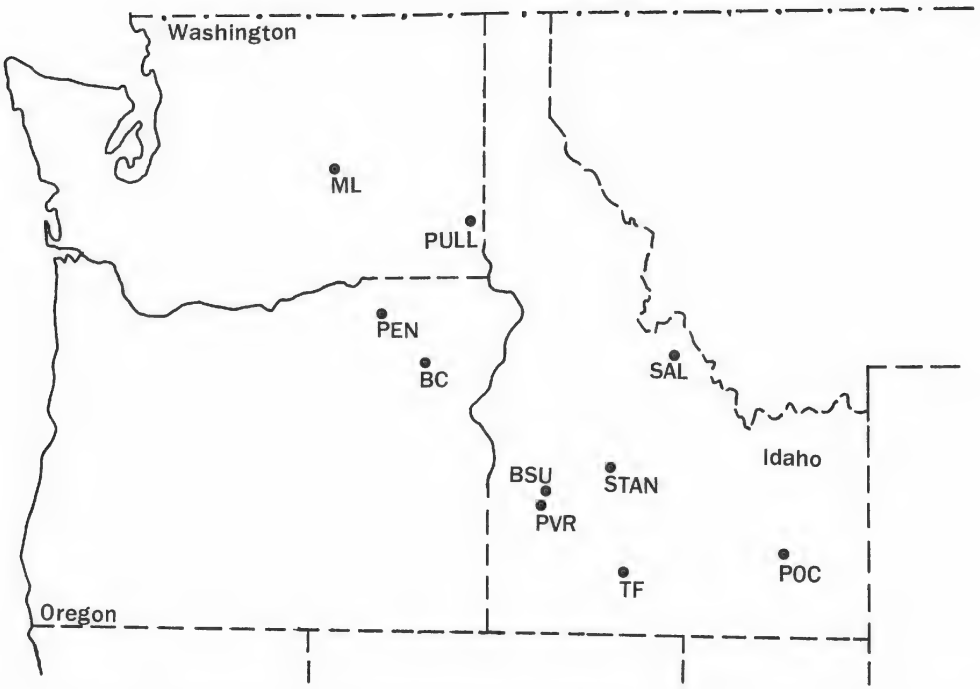

Figure 1. Map of Idaho, Oregon, and Washington, showing the locations of the 10 populations of bulbous bluegrass sampled and analyzed in this study. See Table 1 for names of sampled sites corresponding to the population abbreviations.

TABLE 1. Collection data for bulbous bluegrass population from Idaho, Oregon, and Washington, population abbreviations, and a general description of the size, density, and habitat conditions of each collection site.

State	County	Location	Population Abbreviation	Population Description
Idaho	1. Ada	Boise-Boise State University	BSU	large, high density, running path along the Boise River behind Boise State University
	2. Ada	Boise-Pleasant Valley Road	PVR	large, high density, along Pleasant Valley Road near Idaho State Penitentiary
	3. Twin Falls	Twin Falls	TF	medium, moderate density, beneath overpass
	4. Bannock	Pocatello	POC	small, moderate density, vacant lot
	5. Custer	Stanley	STAN	moderate, moderate density, dirt road on west side of Salmon River at Hell Roaring lower trailhead
	6. Lemhi	Salmon	SAL	small, low density, roadside near vacant lot
Oregon	7. Baker	Baker City	BC	large, high density, corner hillside lot
	8. Umatilla	Pendleton	PEN	moderate, high density, roadside near Eastern Oregon State Correctional Institute
Washington	9. Whitman	Pullman	PULL	moderate, moderate density, E.H. Steffen Center
	10. Grant	Moses Lake	ML	large, moderate density, disturbed sagebrush habitat

contained mature bulblets. Mature bulblets are 2 mm in length, and possess broad, shiny, dark purple or black bases with protruding foliaceous tips. One bulblet from each individual in a population was randomly selected and placed on moistened filter paper in a petri dish. To break dormancy, bulbous bluegrass required a chilling treatment consisting of incubating bulblets on moistened filter paper at 5 C for 4-5 days (Ball et al. 1995). Additional water was applied as needed to prevent desiccation of the bulblets. After chilling, petri dishes were incubated at room temperature with moderate sunlight, with bulblets usually "germinating" within 24 hours. "Seedlings" were permitted to grow for approximately one week, prior to genetic analysis.

Genetic Analysis

Enzyme electrophoresis was performed according to the methods of Soltis et al. (1983). Harvested "seedling" tissue was macerated in tris-HCL grinding buffer-PVP solution. Final concentration of PVP (MW 40,000) in the grinding buffer was 12% (w/v). Starch concentration of the gels was 12.5% (w/v). Enzyme activity for alcohol dehydrogenase (ADH), aldolase (ALD), glutamate dehydrogenase (GDH), glutamate oxalacetate transaminase (GOT), malic enzyme (ME), phosphoglucoisomerase (PGI), and triose-phosphate isomerase (TPI) were visualized using buffer system 8 (Novak et al. 1991). Enzyme activity for glyceraldehyde-3-phosphate dehydrogenase (G3PDH), isocitrate dehydrogenase (IDH), malate dehydrogenase (MDH), phosphoglucomutase (PGM), 6-phosphogluconate dehydrogenase (6PGD), and shikimate dehydrogenase (SkDH) were visualized using buffer system 1; while enzyme activity for glucose-6-phosphate dehydrogenase (G6PDH), malate dehydrogenase (MDH), and phosphoglucomutase (PGM) were visualized using buffer system 9 (Soltis, et al. 1983). Reliable interpretation of the banding patterns of MDH and PGM was obtained by comparing results obtained from both system 1 and system 9. Enzyme staining procedures followed the methods of Soltis et al. (1983), except for ADH, which followed Haufler (1985). ALD and TPI were stained using the agarose overlay method.

Enzyme banding patterns for each individual were recorded, and genotypes were inferred based on known enzyme subunit structure and compartmentalization for diploid seed plants (Weeden and Wendel 1989). However, the complex banding patterns observed for bulbous bluegrass were not consistent with diploid gene expression, but instead were more consistent with the patterns previously reported for autotetraploid plant taxa (Soltis and Rieseberg 1986; Soltis and Soltis 1988, Soltis and Soltis 1989a, Soltis and Soltis 1989b, Wolf et al. 1989). Because of these similarities, we assumed that the populations of bulbous bluegrass analyzed in this study are autotetraploid, and assigned genotypes based on the relative staining intensity and number of enzyme bands scored at each polymorphic locus. Additionally, we reanalyzed many individuals to ensure that our assignments of genotypes, based on the criteria described above, were consistent.

Genetic diversity for all 10 populations of bulbous bluegrass was assessed using the mean number of alleles per locus (A), the percent polymorphic loci per population ($\%P$) and the observed mean heterozygosity (H_o). A locus was defined as being polymorphic if one or more individual(s) within a population possessed a genotype that differed from other individuals in that population, at that locus. Observed mean heterozygosity was determined by the direct count method. Mean values for A and $\%P$ for all ten populations of bulbous bluegrass, at both the species and population levels, were compared to the mean values of A and $\%P$ compiled by Hamrick and Godt (1989) from over 400 published studies of plant species using enzyme electrophoresis. Because an autotetraploid individual can maintain as many as three or four alleles at a single locus (due to tetrasomic inheritance), the proportion of individuals exhibiting three or more alleles at one or more locus was calculated for each population (Soltis and Soltis 1989b). In this study, clonal structure was assessed by calculating the total number of unique multilocus genotypes, as well as the distribution of multilocus genotypes within and among populations. Multilocus genotypes were assigned by examining their allelic composition at all polymorphic loci.

Results

Genetic Diversity

A total of 264 bulbous bluegrass individuals from 10 populations in Idaho, Oregon, and Washington were analyzed for genetic diversity, with an average of approximately 26 individuals per

population. All enzyme bands scored in this study migrated anodally from the origin. The 14 enzymes were coded for by 19 putative genetic loci. Across all populations nine of 19 loci (47.4%) were polymorphic: *Adh*, *G3pdh*, *Idh-1*, *Mdh-1*, *Mdh-2*, *Pgi-1*, *Pgi-2*, *Pgm-1*, and *6Pgd-1* (Table 2); all other loci were monomorphic. Although the populations of bulbous bluegrass analyzed in this study generally possessed similar patterns of allelic variability, some differences among populations were observed. For instance, *Adha* was detected in only five of 10 populations (TF, POC, BC, PEN, and ML); whereas, *Adhc* occurred in all populations except PVR, PEN, PULL, and ML. *G3pdhb* was detected in only two populations: TF and STAN. Eight of 10 populations were polymorphic at *Idh-1*, while PVR and PULL were fixed for *Idh-1a*. Only BSU, PVR, and PULL were polymorphic at *Mdh-1*, all other populations were fixed for *Mdh-1a*. With the exception of STAN (which was fixed for *Pgi-2c*) and PEN (with both *Pgi-2b* and *Pgi-2c*), all 10 populations possessed at least three alleles at *Mdh-2* and *Pgi-2*. All 10 populations were polymorphic at *Pgi-1* and *6Pgd-1*. Finally, six of 10 populations were polymorphic at *Pgm-1*, while PVR, POC, PULL, and ML were fixed for *Pgm-1a*.

A total of 34 alleles were detected at the 19 scored loci, with a mean value of 1.79 alleles/locus for the species. Averaged across all populations, the mean value for *A* was 1.54, *%P* was 27.9, and H_o was 0.202 (Table 3). The highest values for *A* and *%P* (1.74 and 36.8%, respectively) were observed in the TF population. The same value for *%P* (36.8%) was found in the BSU and PEN populations, although values for *A* in the latter two populations were slightly lower than TF. By far, the lowest levels of %P (5.3) and A (1.42) were observed in the PVR population, even though PVR also had the second highest H_o value (0.263). The highest value (H_o = 0.309) was detected in the STAN population while the lowest value of 0.124 was observed in the SAL population. Mean values for *A* and *%P* for all ten

TABLE 2. Allele frequencies at nine polymorphic loci for each population of bulbous bluegrass. Population abbreviations are given in Table 1.

		Populations									
Locus	Alleles	BSU	PVR	TF	POC	STAN	SAL	BC	PEN	PULL	ML
Adh	*a*	-	-	0.138	0.268	-	-	0.069	0.057	-	0.052
	b	0.875	1.000	0.793	0.723	0.917	0.971	0.922	0.943	1.000	0.948
	c	0.125	-	0.069	0.009	0.083	0.029	0.009	-	-	-
G3pdh	*a*	1.000	1.000	0.888	1.000	0.750	1.000	1.000	1.000	1.000	1.000
	b	-	-	0.112	-	0.250	-	-	-	-	-
Idh-1	*a*	0.644	1.000	0.517	0.036	0.833	0.118	0.198	0.179	1.000	0.042
	b	0.356	-	0.462	0.964	0.167	0.882	0.802	0.821	-	0.958
Mdh-1	*a*	0.990	0.750	1.000	1.000	1.000	1.000	1.000	1.000	0.946	1.000
	b	0.010	0.250	-	-	-	-	-	-	0.054	-
Mdh-2	*a*	0.317	0.250	0.259	0.375	0.250	0.691	0.405	0.579	0.250	0.281
	b	0.289	0.500	0.207	0.018	0.50	0.059	0.052	0.028	0.500	0.021
	c	0.077	-	0.276	0.232	-	-	0.138	0.143	-	0.281
	d	0.163	0.250	0.103	0.009	0.250	0.029	0.026	0.014	0.250	0.010
	e	0.154	-	0.155	0.366	-	0.221	0.379	0.236	-	0.219
Pgi-1	*a*	0.250	0.250	0.250	0.250	0.350	0.265	0.250	0.329	0.250	0.250
	b	0.750	0.750	0.750	0.750	0.660	0.735	0.750	0.671	0.750	0.750
Pgi-2	*a*	0.038	0.250	0.103	0.116	-	-	0.035	-	0.239	0.031
	b	0.174	0.250	0.009	0.080	0.167	-	0.017	0.186	0.294	0.031
	c	0.750	0.250	0.853	0.804	0.667	1.000	0.948	0.814	0.467	0.938
	d	0.038	0.250	0.035	-	0.167	-	-	-	-	-
Pgm-1	*a*	0.933	1.000	0.922	1.000	0.833	0.971	0.647	0.629	1.000	1.000
	b	0.067	-	0.78	-	0.167	0.029	0.353	0.371	-	-
6Pgd-1	*a*	0.577	0.607	0.638	0.955	0.667	0.912	0.888	0.829	0.641	0.958
	b	0.423	0.393	0.362	0.045	0.333	0.088	0.112	0.171	0.359	0.042

TABLE 3. Genetic variability statistics for bulbous bluegrass populations. Description of *A*, *%P*, and H_o are given in the text. Proportion refers to the number of individuals possessing three or more alleles at one or more loci in these populations.

State	Population	*N*	*A*	*%P*	H_o	Proportion	Multilocus Genotypes
Idaho	1. Boise-BSU	26	1.68	36.8	0.227	0.77	12
	2. Boise-PVR	21	1.42	5.3	0.263	1.00	2
	3. Twin Falls	29	1.74	36.8	0.243	0.97	15
	4. Pocatello	28	1.58	26.3	0.177	0.50	7
	5. Stanley	15	1.53	31.6	0.309	1.00	7
	6. Salmon	34	1.42	31.6	0.124	0.12	3
Oregon	7. Baker City	29	1.58	31.6	0.160	0.38	10
	8. Pendleton	35	1.53	36.8	0.174	0.34	24
Washington	9. Pullman	23	1.37	15.8	0.222	1.00	5
	10. Moses Lake	24	1.53	26.3	0.125	0.33	11
All populations		264	1.54	27.9	0.202	0.64	9.6

populations of bulbous bluegrass, at both the species and population levels, were similar to the mean values of *A* and *%P* compiled by Hamrick and Godt (1989) (Table 4).

The possession of loci with three or more alleles at a locus is one of the genetic consequences of autopolyploidy (Soltis and Soltis 1988, Soltis and Soltis 1989b). Therefore, autotetraploid plants exhibit "enzyme multiplicity" (i.e., they produce multiple enzyme forms, as well as more kinds of hybrid enzymes for multimeric enzymes). For the ten populations of bulbous bluegrass analyzed in this study, enzyme multiplicity was observed at *Mdh-2* and *Pgi-2*. Even though three of these 10 populations of bulbous bluegrass (TF, POC, BC) possessed three alleles at *Adh*, no one individual exhibited enzyme multiplicity at this locus. The mean proportion of individuals having three or more alleles at one or more loci for all ten populations was 0.64 (Table 3). The highest proportion (1.00) occurred within two Idaho populations (PVR and STAN) and one Washington population (PULL), while the lowest proportion (0.12) was found within the SAL population of Idaho. All ten populations possessed individuals exhibiting enzyme multiplicity at *Mdh-2* (with a minimum of four individuals in SAL), while only five of ten populations (BSU, PVR, POC, STAN, and PULL) contained individuals with enzyme multiplicity at *Pgi-2* (data not shown). Every individual in PVR exhibited enzyme multiplicity for both *Mdh-2* and *Pgi-2*.

TABLE 4. Comparison of genetic variability in bulbous bluegrass with other plant species, based on enzyme electrophoresis data. Data for the other plant species were compiled by Hamrick and Godt (1990).

	Species level	
	A	*%P*
Monocots	2.38	59.2
Herbaceous short-lived	1.42	41.3
Temperate plants	1.91	48.5
Gravity-dispersed seeds	1.81	45.7
Asexual and sexual	1.69	43.8
Early successional	1.98	49.0
All other plants	1.96	50.5
Bulbous bluegrass	1.79	47.4
	Population level	
	A	*%P*
Monocots	1.66	40.3
Herbaceous short-lived	1.40	28.0
Temperate plants	1.51	32.6
Gravity-dispersed seeds	1.45	29.8
Asexual and sexual	1.47	29.4
Early successional	1.46	29.6
All other plants	1.53	34.2
Bulbous bluegrass	1.54	27.9

Clonal Structure

A total of 84 multilocus genotypes were detected within the 10 populations of bulbous bluegrass analyzed in this study (Figure 2). Seventy-six multilocus genotypes (90.5%) were restricted to

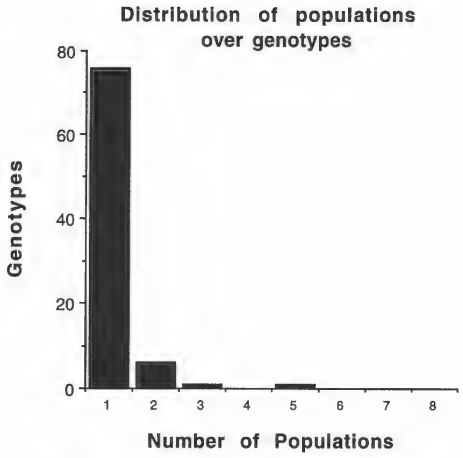

Figure 2. Histogram illustrating the distribution of 84 multilocus genotypes among the 10 populations of bulbous bluegrass. "Number of Populations" equals the number of populations in which each genotype was detected.

a single (but not the same) population. Six different multilocus genotypes were found within two populations, one genotype was found within three, and the most widespread genotype, designated #2, occurred in five of the ten populations (BSU, POC, BC, PEN, and ML). The mean number of populations that each genotype occurred in was 1.17. The fewest number of multilocus genotypes that occurred within a single population (PVR) was two, while the highest number of genotypes found within a population (PEN) was 24 (Table 3, Figure 3). On average, each population of bulbous bluegrass included in this analysis possessed 9.6 multilocus genotypes (Table 3).

Discussion

Genetic Diversity

Our analysis of these 10 populations of bulbous bluegrass from Idaho, Oregon, and Washington indicates that this species displays surprisingly high levels of genetic diversity at the species and

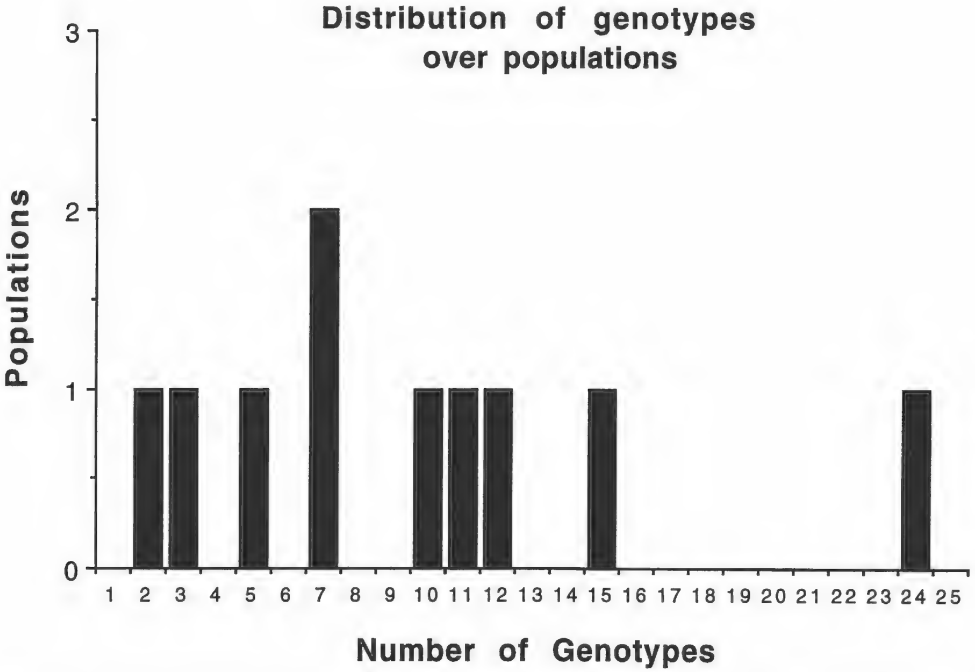
Distribution of genotypes over populations
Populations
3
2
1
0
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25
Number of Genotypes

Figure 3. Histogram displaying the number of genotypes detected in each of the 10 populations of bulbous bluegrass. "Populations" equals the actual number of sites with a given number of genotypes.

population level. At the species level, the mean values for A and %P reported for bulbous bluegrass (1.79 and 47.4, respectively) are quite similar to the values reported for other plant species (1.96 and 50.5, respectively) (Table 4). At the population level, similar mean values of *A* were detected for bulbous bluegrass and other plants (1.53 and 1.54, respectively), while the mean value of *%P* for bulbous bluegrass (27.9) was somewhat lower when compared with other plants (34.2). However, if the results for PVR and PULL (%P = 5.3 and 15.8, respectively) are excluded from the analysis, the value of %P for the remaining eight populations of bulbous bluegrass (32.2) is very comparable to the value reported for other plants. These observations are surprising because most of these other species reproduce sexually, and sexual species are generally believed to possess more diversity than species that reproduce clonally. With the exception of the values for other monocots, bulbous bluegrass has similar amounts of genetic diversity compared to plants with similar life history characteristics, at both the species and population level, as summarized by Hamrick and Godt (1989): herbaceous short-lived perennials, temperate plants, plants with gravity-dispersed seeds, plants that can reproduce both sexually and asexual, and early successional plants (Table 4).

Considering that bulbous bluegrass is an introduced plant species that reproduces by clonal means, the findings of this study are made even more surprising. Low levels of genetic diversity have often been reported within and among populations of introduced plant species (Brown and Marshall 1981, Barrett and Richardson 1986, Barrett and Shore 1989), especially among introduced plants that reproduce clonally (Barrett and Richardson 1986, Barrett and Shore 1989). For instance, the level of genetic variation detected in these 10 populations of bulbous bluegrass was higher than that reported for introduced plants that reproduce sexually such as Noogoora burr (*Xanthium strumarium*—Moran and Marshall 1978), little jack (*Emex spinosa*—Marshall and Weiss 1982), witchweed (*Striga asiatica*—Werth et. al. 1984), Johnson grass (*Sorghum halepense*—Warwick et. al. 1984), and cheatgrass (*Bromus tectorum*—Novak et. al. 1991, Novak and Mack 1993). In addition, the level of genetic variation in bulbous bluegrass was substantially higher than the level reported for most introduced plants that exhibit clonal reproduction such as skeleton weed (*Chondrilla juncea*—Burdon et. al. 1980), dandelion (*Taraxacum officinale*—Lyman and Ellstrand 1984), and white bryony (*Bryonia alba*—Novak and Mack 1995).

Bulbous bluegrass also possesses high levels of heterozygosity (H_0 = 0.202), and 64% of all individuals, on average, maintained as many as three or more alleles at one or more loci (Table 3). Our findings are consistent with previous reports describing the genetic consequences of autopolyploidy: autopolyploid plants frequently possess higher levels of heterozygosity, because of enzyme multiplicity, when compared to diploid plants (Soltis and Rieseberg 1986; Soltis and Soltis 1988, Soltis and Soltis 1989a, Soltis and Soltis 1989b, Wolf et al. 1989). Based on the results of this study, and the high chromosome counts commonly reported for bulbous bluegrass, it is likely that this species is an autopolyploid. This likelihood probably explains the higher levels of genetic variation reported for bulbous bluegrass when compared to the other introduced plant species listed above, which are primarily diploids. Further insights into the type of autopolyploidy exhibited by bulbous bluegrass will be obtained by performing chromosomes counts on the populations analyzed in this study.

Clonal Structure

Insights into the clonal structure of bulbous bluegrass are provided by examining the number and distribution of multilocus genotypes. The distribution of multilocus genotypes within and among populations of this grass is in general agreement with results reported for other clonal plant species (for a review see Ellstrand and Roose 1987). The vast majority of genotypes (76 of 84) possessed a local distribution, being restricted to just a single (although not the same) population, and the most widespread multilocus genotype (#2) was detected in only five of 10 populations (BSU, POC, BC, PEN, and ML). In addition, none of the multilocus genotypes detected in multiple populations appeared to have a strong geographical pattern to their distribution. However, several of these genotypes were consistently detected in either the BSU, POC, BC, or ML populations, with three of these populations (BSU, BC, and ML) located in western portions of the sampled range. For instance, genotype #4 was detected in BSU and ML, genotype #7 was detected in BSU and BC, and genotype #19 was detected in BC and ML (data not shown). The abundance and distribution of these multilocus genotypes may have resulted from multiple introductions of this grass into the area

sampled and its subsequent accidental spread. Alternatively, this abundance and distribution may have resulted from multiple introductions and subsequent purposeful introduction of the grass to prevent soil erosion or control of more troublesome weeds. Purposeful introductions are a more likely means of spread because bulbous bluegrass bulblets appear to possess limited dispersal capabilities.

Bulbous bluegrass did not have a single population that was uniclonal (Table 3). The fewest number of genotypes detected within a single population (PVR) was two, while 24 different genotypes were detected in the PEN population. These 24 distinct genotypes were detected from a total of 36 individuals, indicating a high level of diversity within this population. These findings are in general agreement with the results reported for other clonal plant species. In their analysis of 27 studies, Ellstrand and Roose (1987) reported that the percentage of multiclonal populations per study tended to be high, with a mean of 77% and a range of 0-100%. The results obtained for bulbous bluegrass are clearly at the high end of this range. Ellstrand and Roose (1987) also reported that the average number of genotypes detected per population was 16.1 However, this value is inflated because one of these species possessed 167 genotypes per population, and if this value is eliminated from their calculation the average number of genotypes per population is reduced to 10.8 The number of genotypes detected per population for bulbous bluegrass is similar to the value reported above: on average, each population possessed 9.6 multilocus genotypes (Table 3).

The number of multilocus genotypes that bulbous bluegrass possesses is remarkably high for an introduced clonal species. Theory predicts that the number of genotypes detected is positively correlated with the number of individuals analyzed per population, and the number of characters (loci) employed (Ellstrand and Roose 1987, Bayer 1990). The large number of multilocus genotypes (clones) detected in this study may be due to the fact that we analyzed, on average, 26 individuals per population, and scored variability in these populations using the results of nine polymorphic loci. A slightly higher number of characters were employed for the identification of clones in the studies summarized by Ellstrand and Roose (1987): on average, 11 characters were used.

In addition, such high levels of genetic variation for this species may also be due to several other factors: 1) multiple introduction of different genotypes may have occurred directly into these locations, and/or 2) some sexual reproduction may have occurred within various locations in its introduced range even though all of the reproductive structures analyzed from these populations were bulblets.

Conclusions

Bulbous bluegrass possesses a large amount of genetic diversity despite the widely held belief that clonal species do not possess as much diversity as sexual ones. Therefore, our results are in general agreement with the second group of models described above, and suggest that clonal species are capable of possessing as much genetic diversity as sexual species (Maynard Smith 1971, Lynch 1984, Ellstrand and Roose 1987). Multiple introduction events are a likely cause of the high level of genetic diversity within populations and the restricted distribution of multilocus genotypes among populations. These results join a growing body of genetic evidence that suggests multiple introductions of an alien species may be more common than previously thought. In addition, a small amount of sexual reproduction may also have contributed to the high level of genetic diversity observed for this species. Finally, it is interesting to note that the role of introduction events, sexual reproduction, and autopolyploidy in off-setting the anticipated loss of genetic variation in these populations can only be fully resolved by the analysis of populations from the native range. As this project expands, it should also include the analysis of Eurasian populations of bulbous bluegrass.

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Seasonal Variation in California Bighorn Ram (*Ovis canadensis californiana*) Habitat Use and Group Size

Abstract

Seasonal changes in bighorn sheep (*Ovis canadensis*) habitat use and social systems can create profound management challenges. We studied spring-summer distribution, habitat use, and group size of California bighorn rams on Poker Jim Ridge, Oregon. Ram groups were observed during April-August 1990. Herd range was smaller in spring (24.4 km^2) than summer (74.5 km^2). Ram groups were closer to escape terrain ($P < 0.001$), farther from water ($P < 0.001$), on gentler slopes ($P = 0.01$) and at higher elevations ($P < 0.001$) in spring. Distance to escape terrain and distance to water were significant main effects differentiating spring and summer habitat use ($P < 0.001$). Ram group size varied by month ($P < 0.001$), with groups in July-August smaller than those in April-June ($P < 0.01$). Seasonal changes in ram distribution appeared to be associated with changing habitat conditions, particularly water availability. Small group sizes in late summer probably reflected resource limitations, and occurred in spite of use of less secure habitats during this period. Managers of bighorn sheep populations should consider the unique requirements of their populations under a variety of environmental conditions, and provide adequate protection to sustain seasonal shifts in distribution.

Introduction

Habitat quality in arid ecosystems can vary greatly between seasons, and is largely determined by precipitation regimens that control forage and water availability (Beatley 1974, Douglas and Leslie 1986, Wehausen et al. 1987). Numerous studies have shown that seasonal shifts in bighorn sheep distribution are related to changing habitat conditions (e.g., Welles and Welles 1961, Shannon et al. 1975, Leslie and Douglas 1979, Krausman and Leopold 1986, Krausman et al. 1989). These shifts presumably increase fitness by satisfying requirements for forage, water, thermal protection, escape cover, and areas for bedding, lambing and rutting (Shannon et al. 1975, Wilson et al. 1980, Tilton and Willard 1982). Bighorn sheep generally select open areas providing good visibility, adequate forage and access to escape terrain (Buechner 1960, Geist 1971, Risenhoover and Bailey 1985, Wakelyn 1987). During dry seasons or droughts, however, water availability may be a more important determinant of habitat selection (Welles and Welles 1961, Leslie and Douglas 1979). Sex-specific differences in habitat requirements (Blood 1963, Woolf et al. 1970, Geist 1971, Geist and Petocz 1977, Leslie and Douglas 1979, Morgantini and Hudson 1981, Gionfriddo and Krausman 1986, Krausman et al. 1989, Bleich et al. 1997) can result in different responses to seasonal changes in habitat condition between rams and ewes.

Bighorn sheep group sizes also reflect changing habitat conditions. Sheep may form smaller groups when resources are limited, thus avoiding resource depletion (Leslie and Douglas 1979, Berger 1979). Group size may also be a function of vegetative and physiographic structure; the formation of large groups enhances predator surveillance, allowing sheep to use habitats farther from escape terrain or with decreased visibility (Risenhoover and Bailey 1985, Warrick and Krausman 1987, Krausman et al. 1989).

Our objective was to describe seasonal shifts in bighorn ram distribution in relation to use of physiographic and vegetative habitat components. We also examined trends in group size over time, and hypothesized that group size would decrease during late summer in response to declining resources.

Study Area

The study was conducted on Poker Jim Ridge (PJR) (42°N, 119°W), a fault block mountain that comprised 89 km^2 of the northern portion of Hart Mountain National Antelope Refuge in Lake County, southeastern Oregon. The main axis of the ridge was oriented north-south. The west side rose precipitously from the Warner Valley (1,366 m) to a maximum elevation of 1,961 m. The top of PJR was a rolling plateau ≤2 km wide. The east side sloped gradually down to the Catlow

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Valley (1,555 m). Yearly precipitation averaged 27.0 cm, with the majority occurring as winter and spring snows. Water was available only in small ephemeral pools and two more reliable sources: Rock Creek, in the Catlow Valley ≥5 km east of the rim of PJR, and Petroglyph Lake, on the south end of PJR 1 km from the rim. Nineteen-ninety was a relatively dry year (19.0 cm precipitation) and Rock Creek was dry by mid-August. Vegetation was typical of the shrub-steppe communities described by Franklin and Dyrness (1973), which include sagebrush (*Artemisia tridentata*)-bunchgrass associations and stands of western juniper (*Juniperus occidentalis*). Forty-six adult and subadult rams ≥2 yr-old occupied PJR during 1990; a population of ewes, lambs and yearlings occupied the range for part of the year, but migrated elsewhere June-September (Payer 1992).

Methods and Materials

Bighorn ram groups were defined as groups consisting of adult and subadult males only. Ram group size and habitat use were assessed during 7 April to 31 August 1990 using direct observations of animals from 4 predetermined, non-overlapping routes. Each route was traveled 1 day per week. Ram group locations were plotted on U.S. Geological Survey 7.5-minute series topographic maps (1:24,000). We used the maps to measure elevation, slope (%), aspect (north, east, south, or west, corresponding to 315°-44°, 45°-134°, 135°-224° and 225°-314°, respectively), distance to water (= $[x^2 + y^2]^{0.5}$, where x = horizontal distance and y = vertical distance, respectively) and distance to escape terrain (similarly calculated) for each group location. Escape terrain was defined as "steep rocky terrain on which mountain sheep would safely outdistance or outmaneuver predators" (Gionfriddo and Krausman 1986). Escape terrain was characterized by rugged terrain or cliffs with slope >60%, and was present in a nearly contiguous 16-km x ≥0.5-km band on the west side of PJR. We surveyed and mapped escape terrain and water sources during August 1990.

We recorded habitat type and, when possible, number of individuals for each ram group observation. Habitat type definitions were based on vegetative and physiographic features thought to be important to bighorn sheep, including dominant grass and shrub species, presence and density of trees, and steepness (Buechner 1960, Geist 1971, Shannon et al. 1975, Risenhoover and Bailey 1985, Wakelyn 1987).

Mean herbaceous and shrub species canopy cover, shrub height, and shrub density were estimated for each habitat type by methods similar to those of Poulton and Tisdale (1961). We established 3 50-m line transects in representative stands of vegetation within each habitat type during June 1991, at peak forb abundance. Percent herbaceous cover was visually estimated within 20-cm x 50-cm plots placed every 5 m along each transect (Daubenmire 1959). The number of shrubs rooted in a 1-m belt adjacent to each transect was counted to estimate shrub density. Mean shrub height was calculated by measuring the individual shrub nearest each 5-m point on each transect. Percent canopy cover of shrubs was determined by the line intercept method (Canfield 1941).

In habitats with trees, we estimated tree density by the nearest neighbor method (Cottam and Curtis 1956). We randomly selected 50 trees/habitat and measured distance to the nearest tree. We calculated density as $2d^{-2}$, where d was the mean distance between nearest neighbors.

We used the minimum convex polygon method (Southwood 1966) with group locations as individual fixes to characterize herd ranges during spring (7 April-10 June) and summer (11 June-31 August). Chi-square contingency table analyses were used to compare frequency distributions of habitat type use, distance to escape terrain, distance to water, slope and elevation between seasons. We excluded aspect because it varied little over the area occupied by rams. If $P < 0.05$, we constructed 95% simultaneous confidence intervals using the Bonferroni approach (Neu et al. 1974) to determine which habitats or physiographic attributes were used differently between seasons. Because these analyses were limited to comparisons between seasons (i.e., this was not a use/availability study), the areal extent of each habitat feature was not considered.

We used logistic regression (Meyers 1990:317-332) to model seasonal change in use of physiographic characteristics. Potential explanatory variables were distance to escape terrain, distance to water, slope and elevation. Season (spring or summer) was the response variable. We constructed a full model with main effects, quadratic

terms, and 2-way interactions, then eliminated variables in a step-wise fashion if $P > 0.05$ (Baker and Nelder 1985). Performance of reduced models was assessed by examination of the -2 log likelihood statistic for the contribution of explanatory variables (SAS Institute, Inc. 1990:1088-1089). We also determined the sensitivity (percent of observed event responses with predicted probability of event > 0.50), specificity (similar statistic for no event responses) and overall correct classification rate of the models (SAS Institute, Inc. 1990:1091-1092). If the final model included only 2 main effects, we generated a response surface by plotting the main effects against predicted probability of response to aid in model interpretation (Murtaugh 1988).

Mean ram group sizes by month were compared using a one-way analysis of variance. Post hoc pairwise comparisons were made with Scheffe's procedure (Milliken and Johnson 1992:35-36).

Results

Habitat Use

We identified 6 habitat types: Low sagebrush (*Artemisia arbuscula*) plateau (LSP), low sagebrush-bunchgrass (LSB), cliff-shrub (CS), juniper-low sagebrush (JLS), juniper-mountain big sagebrush (*Artemisia tridentata vaseyana*) (JMBS), and Wyoming big sagebrush (*Artemisia tridentata wyomingensis*)-bunchgrass (WBSB) (Table 1). The LSP habitat type occupied the PJR plateau above 1,830 m. The LSB habitat type occurred on the PJR plateau below 1,830 m, and on the gentle east-facing slopes above Catlow Valley. The CS habitat type was found on the precipitous west face of PJR, and included the escape cover available to rams on this range. Much of the CS habitat type was bare rock, but vegetation occurred on narrow horizontal benches and in some gullies. The JLS and JMBS habitat types were found at mid- to low elevations on the east side of PJR, and were characterized by an overstory of western juniper with a sagebrush-bunchgrass understory. They differed primarily in tree density (9.7 vs. 90.8 trees/ha in the JLS and the JMBS, respectively) and the nature of the understory. The JMBS habitat type occurred in association with small canyons and rocky breaks. The WBSB habitat type occupied the floor of Catlow Valley near Rock Creek.

We observed 60 and 94 ram groups during spring and summer, respectively. In spring, rams generally occupied the upper PJR plateau <2 km from the rim. In mid-summer they expanded their range to include the east slopes and Catlow Valley near Rock Creek, which was a water source. When the creek went dry in mid-August, ram distribution shifted to the south end of PJR in the vicinity of Petroglyph Lake, which was a late summer water source. Observed spring and summer herd ranges were 24.4 and 74.5 km^2, respectively.

Ram habitat use differed between spring and summer ($X^2 = 34.4$, 5 df, $P < 0.001$) (Figure 1). The LSP habitat was used more frequently in spring, and the JLS and WBSB habitats were used

TABLE 1. Characteristics of shrubby and herbaceous vegetation in bighorn ram (*Ovis canadensis californiana*) habitats on Poker Jim Ridge, Oregon, June 1991.

	Shrubs			Grasses	Forbs
Habitat	Total Canopy Cover (%)	Density (no./m2)	Mean Height (cm)	Total Canopy Cover (%)	Total Canopy Cover (%)
Low sagebrush (*Artemisia arbuscula*) plateau	17.8	1.9	16.8	8.1	16.8
Low sagebrush-bunchgrass	20.7	1.4	23.3	15.0	18.3
Cliff-shrub[a]	32.1	1.8	27.2	6.2	8.4
Juniper (*Juniperus occidentalis*)-low sagebrush	17.6	1.4	23.4	25.5	15.6
Juniper-mountain big sagebrush (*Artemisia tridentata vaseyana*)	25.9	0.7	82.0	7.3	12.1
Wyoming big sagebrush (*Artemisia tridentata wyomingensis*)-bunchgrass	14.9	0.8	50.1	11.9	4.6

[a]Results reflect characteristics within islands of vegetation.

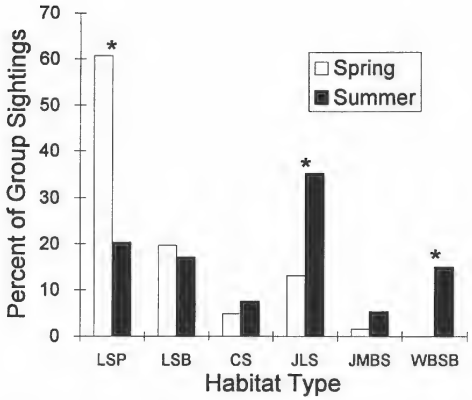

Figure 1. Percent use of habitat types by bighorn ram (*Ovis canadensis californiana*) groups on Poker Jim Ridge, Oregon, spring and summer 1990. LSP = low sagebrush (*Artemisia arbuscula*) plateau, LSB = low sagebrush-bunchgrass, CS = cliff-shrub, JLS = juniper (*Juniperus occidentalis*)-low sagebrush, JMBS = juniper-mountain big sagebrush (*Artemisia tridentata vaseyana*), WBSB = Wyoming big sagebrush (*Artemisia tridentata wyomingensis*)-bunchgrass. * = Significant difference in use between spring and summer based on 95% simultaneous confidence intervals.

more frequently in summer. The CS and JMBS habitats received little use in either season.

Significant differences were found in use of physiographic characteristics between spring and summer (Figure 2). Ram groups were found closer to escape terrain in spring ($\underline{X}^2 = 17.6$, 3 df, $\underline{P} < 0.001$). Sixty-five percent of spring locations but only 40% of summer locations were within 1 km of escape terrain. We commonly observed rams >3 km from escape terrain in summer (25.5% of summer locations). In spring, rams tended to be farther from water ($\underline{X}^2 = 26.5$, 3 df, $\underline{P} < 0.001$), on gentler slopes ($\underline{X}^2 = 9.16$, 2 df, $\underline{P} = 0.01$), and at higher elevations ($\underline{X}^2 = 19.32$, 2 df, $\underline{P} < 0.001$).

The most parsimonious logistic regression model for differentiating use of physiographic characteristics between spring and summer included main effects and quadratic terms for distance to escape terrain and water, and a significant distance-to-escape terrain x distance-to-water interaction (Table 2). The contribution of the variables to the fitting of the model was significant ($\underline{X}^2 = 50.66$, 5 df, $\underline{P} < 0.001$). The addition of elevation to this model significantly decreased model deviance ($\underline{X}^2$ approximation = 6.48, 1 df,

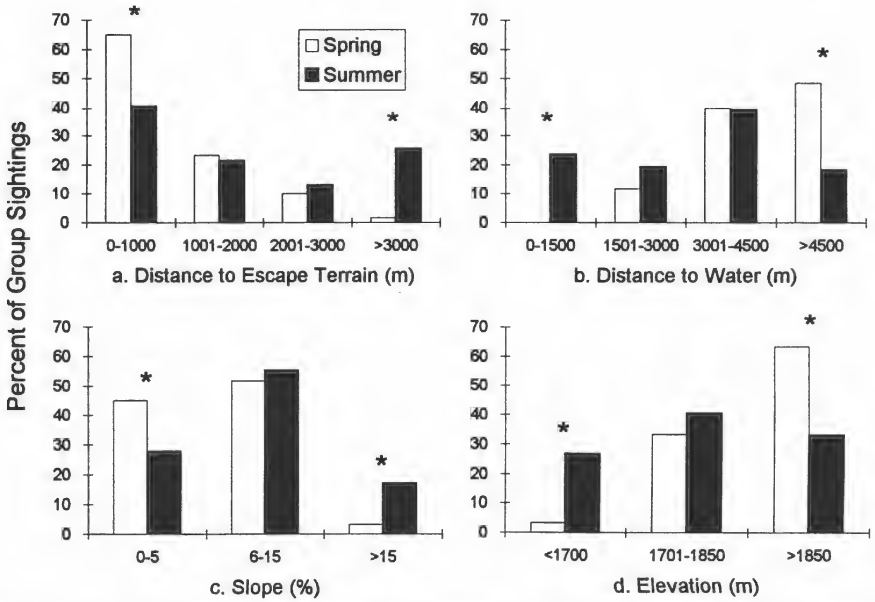

Figure 2. Comparison of bighorn ram (*Ovis canadensis californiana*) group distribution on Poker Jim Ridge, Oregon between spring and summer 1990 in relation to (a) distance to escape terrain, (b) distance to water, (c) slope, and (d) elevation. * = Significant difference in use between spring and summer based on 95% simultaneous confidence intervals.

TABLE 2. Estimated coefficients from logistic regression of probability of a bighorn ram (*Ovis canadensis californiana*) group observation on Poker Jim Ridge, Oregon in spring and summer 1990 occurring in spring against distances to escape terrain (m) and water (m).

Variable	Estimated Coefficient	Standard Error
Intercept	-14.33	5.129
Distance from escape terrain	9.151×10^{-3}	3.100×10^{-3}
(Distance from escape terrain)^2	-1.475×10^{-6}	5.145×10^{-7}
Distance from water	4.378×10^{-3}	1.774×10^{-3}
(Distance from water)^2	-2.741×10^{-7}	1.623×10^{-7}
(Distance from escape terrain) x (Distance from water)	-1.521×10^{-6}	4.997×10^{-7}

$P = 0.011$), but elevation was highly correlated with distances to escape terrain and water (Pearson's $r = -0.820$ and 0.829, respectively). The standard errors of the coefficients of the other variables decreased substantially when elevation was dropped, further emphasizing the collinearity. Sensitivity, specificity and overall correct classification rate of the model were 72.1%, 71.4% and 71.7%, respectively. A response surface generated by plotting distances to escape terrain and water against the predicted probability of a ram group observation occurring in spring demonstrated that ram groups were predicted to most likely occur <2 km from escape terrain and >6 km from water sources during spring (Figure 3). Areas farther from escape terrain and closer to water were predicted to be used more during summer.

Group Size

We observed 1,139 rams in 146 groups. Ram group size varied by month ($F = 13.87, 4, 141$ df,

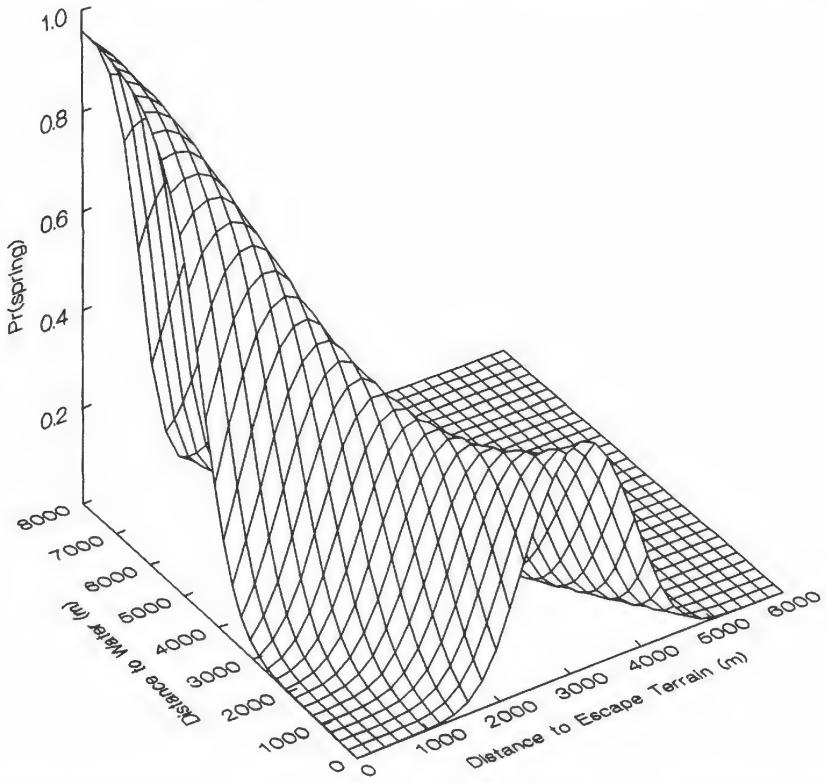

Figure 3. Response surface generated from logistic regression model for differences in distance to escape terrain and water for bighorn ram (*Ovis canadensis californiana*) groups on Poker Jim Ridge, Oregon between spring and summer 1990. Pr(spring) = predicted probability of a group observation at a site described by the response surface occurring in spring.

TABLE 3. Mean size of bighorn ram (*Ovis canadensis californiana*) groups by month, April through August 1990, Poker Jim Ridge, Oregon.

Month	N ram groups encountered	Mean group size (± s.d.)[a]
April	26	12.19 (± 7.32)*
May	24	10.67 (± 6.26)*
June	29	10.03 (± 7.66)*
July	43	4.21 (± 2.91)**
August	24	3.92 (± 3.20)**

[a]Asterisks indicate results of Scheffe's test for pairwise comparisons. Means with different numbers of asterisks are significantly different ($P < 0.05$).

$P < 0.001$) (Table 3). There were no significant pairwise differences between mean group sizes in April, May and June ($P > 0.70$ for all comparisons), or July and August ($P > 0.90$). Ram groups were smaller during July-August than April-June ($P < 0.01$ for all pairwise comparisons).

Discussion

Bighorn ram herd range size increased three-fold between spring and summer. We observed no distinct migration, but rather a gradual expansion into contiguous areas. Herd range size is a function of individual home ranges within a herd and the degree of overlap between those ranges. Bighorn sheep are gregarious (Blood 1963, Simmons 1980), and home ranges within a herd can overlap considerably (Leslie and Douglas 1979). Thus, increased herd range size probably reflected increases in home range size, rather than dispersal of individuals or small groups.

Habitat quality, determined by the availability and juxtaposition of forage, water and escape terrain, is an important determinant of seasonal home range size in bighorn sheep (Krausman et al. 1989). On PJR, escape terrain was obviously constant, but forage and water availability generally decreased from spring to summer. Herd range size increased during the period, consistent with the hypothesis that resource limitations cause bighorn sheep to range over larger areas to satisfy physiological needs (Leslie and Douglas 1979).

The logistic regression model we developed for differentiating use of physiographic characteristics identified variables that explained the majority of variation between seasons. No causality was inferred from the model itself, but knowledge of physiological and behavioral requirements of bighorn rams and the availability of resources on PJR allowed speculation regarding reasons for observed differences. The model was limited by the explanatory variables chosen for inclusion, and obviously other biotic and abiotic factors (e.g., visibility, forage composition and quality) could have affected ram distribution. However, slope, elevation, aspect, and proximity to escape terrain and water are known to be important determinants of habitat use (Shannon et al. 1975, Tilton and Willard 1982, Risenhoover and Bailey 1985, Gionfriddo and Krausman 1986, Krausman and Leopold 1986, Fairbanks et al. 1987, Wakelyn 1987), and bighorn sheep are opportunistic foragers, adapting their diet to available plant communities (Keating et al. 1985, Miller and Gaud 1989). Thus, we chose not to include vegetative association as a potential explanatory variable in the model. We defined habitat types based on physiographic and vegetative features, however, so differences in use of habitat types between seasons provided additional insight into differential use of habitat.

Observed movements of PJR rams between spring and summer probably resulted from changing water requirements associated with changes in forage succulence and availability of ephemeral water sources. In mid-summer, ram activity shifted from the upper plateau to the east slopes and Catlow Valley near Rock Creek. In late summer, Rock Creek dried up and use shifted toward Petroglyph Lake. The lake was much less remote, being within sight of the refuge access road and receiving some human use, but was closer to escape terrain. The former may have contributed to its being a "second choice" water source, while the latter may have helped to offset effects of human disturbance.

Distances to water and escape terrain were significant explanatory variables in the final model differentiating spring and summer habitat use (Table 2). The response surface generated by this model over the range of observed values for explanatory variables demonstrated that the model predicted movement of rams away from the upper plateau (close to escape terrain, far from water) toward Rock Creek (far from escape terrain, close to water) and Petroglyph Lake (close to escape terrain and water) in summer (Figure 3) (note that pr[spring] on the z-axis is equivalent to 1-pr[summer]).

Differences in use of habitat types between spring and summer (Figure 1) also reflected the trend of dispersal from the upper plateau (predominantly LSP) in early summer and utilization of Rock Creek, which was within the WBSB habitat type. Use of JLS also increased during summer. This habitat type provided thermal cover, had the greatest grass canopy cover of any PJR habitat (Table 1), and may have held succulent forage longer due to favorable microclimates created by shade of juniper trees. Mean tree density was relatively low (9.7 trees/ha), so visibility was probably not substantially compromised. Use of the JMBS habitat type did not differ between seasons, even though it was interspersed with JLS habitat type. Mean tree density here was much greater (90.8 trees/ha) and grass canopy less (Table 1), making it a less suitable bighorn sheep habitat (Shannon et al. 1975, Tilton and Willard 1982, Wakelyn 1987).

Ram group size during April-June was more than twice that during July-August (Table 3). Festa-Bianchet (1986) hypothesized that large spring concentrations of Rocky Mountain bighorn rams (*Ovis canadensis canadensis*) in Alberta provided opportunities to develop social skills important for future reproductive success. Other studies have suggested that group size is an indicator of habitat quality, with high quality forage conditions favoring larger groups (Berger 1979, Leslie and Douglas 1979, Simmons 1980). We observed smaller groups during summer when resources were probably more limited, consistent with the latter theory.

It has also been suggested that larger groups enhance predator surveillance, allowing sheep to spend more time foraging and to use habitats farther from escape terrain or with decreased visibility (Risenhoover and Bailey 1985, Warrick and Krausman 1987, Krausman et al. 1989), although there may be little added benefit beyond 5 individuals (Berger 1978). On PJR group size declined coincident with use of less secure habitats, i.e. those further from escape terrain with greater shrub height (WBSB) and presence of trees (JLS). In no month was the upper bound of the 95% confidence interval for mean group size <5, however (Table 3). During this study there were no known predators of adult bighorn sheep on PJR other than humans during 2 1-week hunting seasons in September (W. Pyle, U. S. Fish Wildl. Serv., pers. comm.), and most of the ram range was remote and received little human use. These factors probably released rams from the constraints often associated with use of less secure habitats, allowing them to adapt group size to available resources.

Our data suggested that water availability exerted a major influence on the seasonal distribution of bighorn rams in this population. Rams traveled >5 km from escape terrain and used habitats with reduced visibility to obtain water. We attributed this to a lack of predators and minimal human disturbance. Although bighorn rams may tolerate moderate predation risk to obtain access to high quality habitat, disturbance and habitat degradation due to recreation or cattle grazing could have deleterious effects on a seasonally shifting population (Bleich et al. 1997). Further, seasonal shifts in distribution are unlikely to be rigidly repeated, but rather respond dynamically to changing environmental conditions (Leslie and Douglas 1979, Festa-Bianchet 1986). If this study had been conducted in a year when Rock Creek remained a reliable water source through late summer, for instance, the importance of Petroglyph Lake may not have been realized. Thus it is important to identify habitat requirements under a variety of environmental conditions, and provide adequate protection to sustain seasonal shifts in distribution.

Acknowledgements

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Coyote (*Canis latrans*) Habitat Selection in Urban Areas of Western Washington via Analysis of Routine Movements

Abstract

Habitat preference is often determined by examining temporally independent animal location data with little attention paid to movement behavior. In 1989 - 90, I examined coyote habitat preference in urban areas of Washington State by examining habitat used by 6 radio-collared coyotes during routine movements. I represented routine movements as straight lines connecting consecutive radio-relocations taken at 1-hour intervals during a series of 6-hour tracking sessions. I used compositional analysis to determine if coyotes selected for particular habitat types at 2 spatial scales: i) home range from within an arbitrarily defined study area containing all home ranges and ii) areas used during routine movements from within the home range. There was no difference ($P = 0.631$) in habitat composition between the home ranges and the study area. However, based on habitat availability in home ranges, coyotes preferred ($P < 0.036$) Forest = Shrub > Densely mixed vegetation > Moderately mixed vegetation > Sparsely mixed vegetation during routine movements.

I used stepwise multiple regression to explore the relationship between movement distance and quality of habitat in which the movement began (initial habitat), habitat in which the movement ended (final habitat), habitat gradient (initial - final habitat), and light conditions (night vs. day). Light conditions ($P = 0.006$) and the interaction of light and initial habitat ($P = 0.004$) were significant but weak predictors (multiple $R^2 = 0.137$) of movement distance. Coyotes moved longer distances at night than during the day. Movement distance tended to increase with decreasing habitat quality at night but showed little relationship with habitat quality during the day. Coyotes preferred to travel through, and remain in close proximity to, relatively undisturbed (Forest and Shrub) habitats in urban environments of Washington State.

Introduction

Urbanization dramatically alters natural landscapes and frequently results in a mosaic of small habitat fragments which themselves vary in their degree of disturbance. Perhaps the most obvious change accompanying urbanization is the decrease in the amount of natural vegetation. The largest remaining patches of natural vegetation are typically associated with parks and reserves and often constitute important habitat for mammalian wildlife (Harris 1977, Harris and Rayner 1986). For example, Dickman (1987) recorded as many as 17 species of mammals using small woodland patches in Oxford, England and further showed that species richness in these patches was negatively correlated with several measures of disturbance. However, often it is not clear what role these fragments of vegetation play in the maintenance of urban wildlife populations. In addition, few studies have looked at the way wildlife species use these areas.

The coyote (*Canis latrans*) is a common inhabitant of cities throughout the United States and is often associated with patches of natural vegetation (Gill and Bonnett 1973, Quinn 1995). Urban environments offer a unique opportunity to explore aspects of coyote behavior. For example, does the coyote represent a species that has changed its behavior to exploit urbanized habitat or is it simply a species clinging to remnant patches of natural habitat?

Many studies have explored coyote habitat use patterns by examining temporally independent radio-locations. However, the use of independent observations may limit the type of inference that can be made about coyote behavior because it fails to document how and why animals use an area (Sanderson 1966, Laundré and Keller 1984). Using sequential radio-telemetry data, Laundré and Keller (1981) were able to identify three types of coyote movement patterns that represented three general types of behavior: resting, hunting, and

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traveling behavior. Although Laundré and Keller (1981) did not explicitly study the effect of habitat type on movement behavior, they postulated that specific movement patterns were associated with unique vegetal, faunal, or physiographic characteristics of the home range. To my knowledge there are no studies that have looked at habitat use during routine movements of coyotes where routine movements were defined as movements other than dispersal. The purpose of this study was to explore the relationship between coyote movements and habitat patterns in urban environments.

Methods and Materials

Study Area

The study area was the low elevation (<100 m), portion of King County, Washington (Figure 1). This part of Washington State lies in the wetter region of the Western Hemlock Zone (Franklin and Dryness 1984). Although most of the forest area has been cleared for urban expansion, there are numerous small patches of 40-80-year-old forest consisting primarily of Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), red alder (*Alnus rubra*), big leaf maple (*Acer macrophyllum*), and vine maple (*Acer circinatum*) (Franklin and Dyrness 1984).

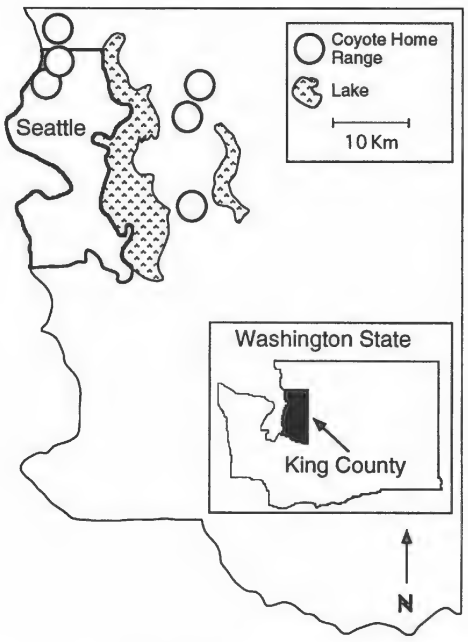

Figure 1. Location of the radio-telemetry study area in the greater Seattle metropolitan area, King County, Washington, 1989-90. The study area was defined as the smallest area containing all coyote relocations. Circles show approximate location of coyote home ranges.

Radio Telemetry

I captured 6 (3 M, 3 F) adult (>1 year old) coyotes using Victor #3 traps with padded jaws during 1989-90. I captured coyotes in the greater Seattle metropolitan area; 3 within 1 km of Seattle's northern border, whose home ranges included part of Seattle, and 3 in urban environments adjacent to Seattle (Figure 1). Each coyote was fitted with a radio transmitter and released at the capture site. During 1990, I followed each coyote during 12, 6-hour, tracking sessions in each of 4 seasons, breeding (1 Jan - 15 Mar), gestation (16 Mar - 30 Apr), pup-rearing (1 May - 31 Jul), and dispersal (1 Aug - 31 Dec). Tracking sessions started at 0600, 1200, 1800, or 2400 with 3 sessions/time period. Consecutive tracking sessions for an individual were separated by ≥24 hours and were typically spaced evenly throughout the season. I located coyotes at 1-hour intervals during a tracking session resulting in 6 locations and 5 movements. I represented movements as straight lines connecting consecutive locations and movement time as the hour the movement was completed (Figure 2). I designated daylight (day) movements as those occurring from 0700-1700 for breeding season, 0700-1900 for gestation season, 0600-2100 for pup-rearing season, and 0700-1900 for dispersal season. All other movements were considered night movements.

Clearly, characterizing coyote movements as straight lines between radio-locations at 1-hour intervals is a simplification that could affect the validity of my study. However, I believe my study approach was appropriate for three reasons. First, I had to chose a time interval to characterize movements that would be long enough to allow an animal to move across a number of pixels so that proportions for *used* and *available* habitat could be calculated, but not so long as to completely obscure important aspects of behavior related to general (all behaviors combined) use

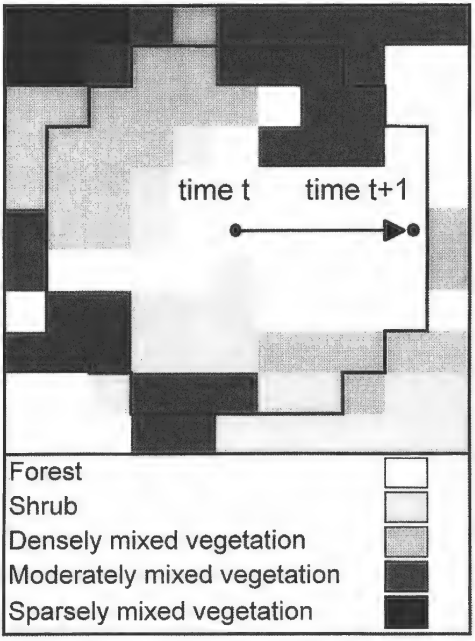

Figure 2. A single coyote movement represented by a straight line connecting relocations taken 1-hour apart. Available habitat during this movement was based on the composition of habitat inside a circle (actually a polygon on raster based maps), outlined here in black, with radius equal to movement distance. Used habitat was based on the composition of habitat intersected by the line connecting points t and t + 1. Each square represents a pixel 28.5 m on a side.

of habitat. Habitat types in my study area tended to occur in patches larger than a single pixel (i.e., pixel types were clumped in their distribution, unpubl. data). Thus to efficiently generate a proportion of *available* habitat that was different (and therefore comparable to *used* habitat) in its composition from a *used* proportion, the movement had to be large relative to the scale of clumping. Second, I had little guidance on appropriate time intervals from published literature since no one to my knowledge had looked at coyote movements as a function of habitat preference in this way and there were no studies of coyote movements in urban habitats to guide me. Finally, I chose the relocation time interval *a priori.* I was conservative in my use of statistics and in making conclusions because I *did* simplify coyote movements. I used a P value of 0.05. I chose not to weight compositional analysis by number of radio locations because it would have made it easier to find pattern (i.e., reject the null hypothesis that habitat use was random).

I obtained radio locations using a Yagi antenna with a 95% error arc ($\theta_{95} \pm 2\ SD$, Springer 1979) of 16.2° (n = 10). I took most (>90%) bearings from locations within 400 m of the animals. At distances of 400 m and with bearings at 90° to each other, the 95% error polygon was approximately 13,071 m^2 (an area represented by 4 x 4 pixels). To minimize actual bearing error, I took three bearings per animal whenever possible and in most cases was able to get very near the animal because of the extent of roads in the urban areas. I found no evidence of bias in my telemetry equipment. Since my study was a comparative one (i.e., use vs. availability) random measurement error should make it more difficult to detect significant differences among use of habitats; that is, more difficult to reject the null hypothesis that use of habitat was proportional to availability.

Geographical Analysis Telemetry Locations

I plotted radio locations of coyotes on 1:24,000-scale topographic maps and assigned Universal Transverse Mercator (UTM) coordinates for each. These coordinates were entered into a database read by Geographical Resources Analysis Support System (GRASS 4.1, U.S. Army Corp. Eng., Construction Eng. Res. Lab. Champaign, Illinois). A GRASS procedure overlays each set of coordinates on an existing geo-referenced base map.

I conducted analyses of telemetry locations in GRASS using a habitat database from a 1985 LANDSAT image of King County. Personnel at the University of Washington Remote Sensing Laboratory used aerial photographs and field verification to classify each pixel, which corresponded to a square parcel 28.5 m on a side, into 1 of 13 different habitats. Overall accuracy (Story and Congalton 1986) of the classified map was 88% (King Co. Open Space Program 1987, King County, Wash., unpubl. data). For this study, I removed freshwater habitat and grouped together other similar types so the study area was represented with 5 habitats (Table 1): (1) Forest—areas dominated (>70%) by trees >6 m in height, >50%

TABLE 1. Proportions of habitat types composing the study area, 100% adaptive kernel home ranges (AKHR), and available habitat during routine movements of coyotes in the greater Seattle metropolitan area, 1989–90. Available habitat for a coyote was based on the composition of habitat inside circles with radius equal to movement distance of that coyote.

	AKHR							Movement Distance (m)		Available Habitat During Routine Movements				
Animal No.	#[a]	Forest	Shrub	Densely Mixed Vegetation	Moderately Mixed Vegetation	Sparsely Mixed Vegetation	#[b]	Mean	(SE)	Forest	Shrub	Densely Mixed Vegetation	Moderately Mixed Vegetation	Sparsely Mixed Vegetation
1	42	0.316	0.219	0.117	0.248	0.100	35	386.2	(54.3)	0.442	0.206	0.080	0.193	0.079
2	72	0.089	0.163	0.149	0.367	0.232	60	402.9	(75.5)	0.129	0.189	0.173	0.313	0.196
3	162	0.065	0.142	0.132	0.390	0.271	135	334.6	(61.9)	0.104	0.176	0.141	0.366	0.213
4	306	0.306	0.212	0.092	0.276	0.113	255	302.0	(53.0)	0.446	0.229	0.057	0.199	0.069
5	144	0.137	0.193	0.153	0.401	0.115	120	124.4	(20.2)	0.202	0.199	0.155	0.322	0.122
6	72	0.115	0.105	0.107	0.407	0.267	60	200.2	(29.3)	0.244	0.221	0.126	0.305	0.104
Habitat composition of the study area														
		0.093	0.124	0.120	0.399	0.264								

[a] Sample size of radio locations on which habitat compositions for AKHRs and the study area were based.
[b] Sample size of movements on which composition of available habitat during routine movements was based.

must be native tree species; (2) Shrub—areas dominated (>50% cover) by any combination of uncut grass, shrubs, or trees 1 - 6 m in height; (3) Densely mixed vegetation—areas dominated (>70%) by any combination of vegetation including shrub and forest, but contained ≤50% shrub cover or 70% tree cover, and ≥50% of the total plant cover was composed of nonnative species. This habitat was characterized by relatively high income housing developments with densities of 1-4 single family houses/ha; (4) Moderately mixed vegetation—areas in which any combination of vegetation types composed 30-70% of total ground cover, ≥50% of the total plant cover consisted of nonnative species, and ≤70% of the total ground cover could be covered by structures and impervious surfaces. This habitat characterized most residential development in King County with densities of 5-12 single family houses/ha; (5) Sparsely mixed vegetation—areas in which any combination of vegetation types composed <30% of the ground area. This habitat characterized most industrial development in King County including downtown metropolitan areas. There were few, if any, single family houses in this habitat.

Compositional Analysis

I used compositional analysis (Aebischer et al. 1993) to compare habitat selection at two spatial scales, i) home ranges versus study area, and ii) discrete areas of use, described either by coyote movement data or telemetry points, versus home ranges. Compositional analysis eliminates many of the common problems associated with habitat selection studies and uses the individual animal rather than a single telemetry location as the experimental unit (Aebischer et al. 1993, Aebischer and Robertson 1994). I used randomization tests provided in MacComp 0.90 (J. P. Carroll, The Game Conservancy, Fordingbridge, Hampshire SP6 1EF United Kingdom) to determine significance levels of Wilk's lambda (L) and t values used in the ranking matrices (Aebischer et al. 1993).

I defined the study area as the smallest area that included all coyote locations. Like many study areas, my study area was somewhat arbitrary because it included areas which were not trapped and were outside study animal home ranges. Using all radio locations for each animal, I calculated 100% adaptive kernel home range estimates (AKHR) (CALHOME, U.S. For. Ser. Pac. Southwest Res. Sta., Albany, CA) for each coyote. Sequential telemetry locations (as described above) were probably autocorrelated and may underestimate true home range size (Swihart and Slade 1985, but see Gese et al. 1990 and Reynolds and Laundré 1990). However, I was interested in delineating a boundary in which I could estimate habitat availability rather than home range size (Quinn 1995). Sequential locations as described above were appropriate for compositional analysis since tracking sessions were distributed in a relatively uniform manner throughout the sampling period (Aebischer et al. 1993:321).

The use of compositional analysis typically assumes equal sampling effort (same number of radio-locations) among animals. One way to account for the effect of unequal sampling effort among animals is to weight each animal's habitat composition by the number of radio-locations for that animal. Although weighting ensures that all animals contribute equally to the test of nonrandom habitat use, weighting might give too much emphasis to frequently observed animals. I chose not to weight samples by the number of radio locations, which resulted in a more conservative test (i.e., more difficult to reject the null hypothesis that habitat use was random (N.J. Aebischer, pers. comm.).

I calculated two estimates of habitat use based on movements: available habitat during movements, and used habitat during movements. For each movement, I defined available habitat as the composition of habitat inside a circle (actually a polygon on raster based maps) whose center was the location of the coyote at time t and whose radius was the movement distance from t to t + 1 (Figure 2). Habitat selection at this scale was akin to asking if coyotes moved in such a way as to remain in proximity to particular habitats types. I defined used habitat as the composition of habitat intersected by the straight line movement (Figure 2).

To estimate movement data habitat composition for a coyote, I summed the number of pixels of each habitat type across all movements (available or used habitat) by that individual and divided by the total number of pixels. An annual estimate was the only time frame for which I could analyze movement data since I did not have enough animals each season (a minimum of 6 is required) to test for seasonal effects (Aebischer et al. 1993). However, before pooling movement data, I determined that there was no difference ($L = 0.708$,

$P = 0.919$) between habitat available at night and habitat available during the day and no difference ($L = 0.798$, $P = 0.9630$) between habitat used at night and habitat used during the day.

Step-wise Regression of Movement Data

I used results from compositional analysis to quantitatively rank habitat quality from 1 to 5 where 1 is most preferred (Forest, Shrub, Densely mixed vegetation, Moderately mixed vegetation, and Sparsely mixed vegetation, respectively; see Table 2 for tests of significance among habitat types). I used stepwise multiple regression to examine the relationship between movement distance and quality of habitat in which the movement began (initial habitat), habitat in which the movement ended (final habitat), habitat gradient (initial - final habitat), and light conditions (night vs. day). The regression was designed to answer the question: are coyotes more likely to move long distances when they were in less preferred habitats. I initially used three different methods of calculating habitat quality: 1) the value of the single pixel in which an animal was located; 2) the sum of values for the nine pixel group (pixel in which the animal was located plus the eight surrounding pixels), and the mode of the nine pixel group. The idea behind using the sum and mode of a nine pixel group is that an animal may be responding to the "value" of habitat at larger scales than a single pixel. In other words, 9 pixels (3 x 3) of forest cover might be more preferred (affect movement distance more) than 9 pixels consisting of 5 forest and 4 moderately mixed vegetation. However, I excluded the 9 pixel sum and mode from further analysis because these measures were correlated ($r > 0.7$) with their single cell analogues (i.e., pixel types tended to be clumped in their distribution). I used a stepwise multiple regression on the pooled data set (all coyotes combined). I pooled movement data of all individuals based on results from compositional analysis, which indicated that habitat selection occurred at the level of my sample population.

The stepwise model fitting program used an alpha = 0.15 (F-test) to enter and remove predictors from the regression equation (Wilkinson 1992). I natural log-transformed the dependent variable [ln(movement distance +1)] to reduce the number of outliers, improve normality, linearity, and homoscedsticity of residuals (Sokal and Rohlf 1981). I removed 11 outliers after examining Studentized residuals resulting in a sample size of $n = 659$. Although some outliers are expected with a large data set such as this, all outliers I removed underestimated movement distance and skewed the distribution of residuals.

TABLE 2. Compositional analysis results for models comparing availability in the 100% adaptive kernel home range (AKHR) with 3 measures of habitat use within the home range: available habitat during movements, used habitat during movements, and habitat use based on telemetry points. Available habitat for a coyote was based on the composition of habitat inside circles with radius equal to movement distance for that coyote. Used habitat was based on the composition of habitat described by lines connecting consecutive relocations of a coyote at 1-hour intervals. Habitat types (Forest = FOR., Shrub = SHR, Densely mixed vegetation = DMV, Moderately mixed vegetation = MMV, and Sparsely mixed vegetation = SMV) are ranked in order of preference from left to right and are underlined when not different ($P > 0.05$) from each other.

Model Tested	P Value[a]	Individual Contrasts				
AKHR vs. Available Habitat	0.0360	FOR	SHR	DMV	MMV	SMV
AKHR vs. Used Habitat	0.0001	FOR	SHR	DMV	MMV	SMV
AKHR vs. Telemetry Points	0.0541	FOR	SHR	DMV	MMV	SMV

[a] P value is the probability that use of habitats was equal to availability of habitats for that model.

Results

I analyzed approximately 1 season of telemetry data (72 locations) from each of 3 coyotes, 2 seasons from each of 2 coyotes, and 4 seasons from 1 animal representing 11 coyote-seasons; 3 each from breeding, gestation, and pup-rearing seasons, and 2 from dispersal season. This represented 798 locations and 665 1-hour movements (Table 1). Animals for which I had <4 seasons of data either dispersed from the study area or died.

Compositional analysis revealed that coyotes established their home ranges at random ($L = 0.413$, $P = 0.631$) within the study area, which was composed of 9.3% Forest, 12.4% Shrub, 12.0% Densely mixed vegetation, 39.9% Moderately mixed vegetation, and 26.4% Sparsely mixed vegetation (Table 1). There was no difference ($L = 0.099$, $P = 0.205$) between available habitat and used habitat during movements. However, available habitat and used habitat during movements were different from expected based on the composition of home ranges ($L = 0.0340$, $P = 0.036$, $L = 0.0567$, $P < 0.0001$, respectively). Coyotes moved in such a way that available habitat and used habitat contained more Forest, Shrub, and Densely mixed vegetation and less Moderately and Sparsely mixed vegetation than the home range as a whole (Table 2). Habitat use based on telemetry points was not different from expected based on composition of home ranges ($L = 0.0420$, $P = 0.0541$; Table 2).

Of the 644 moves, 253 (39%) originated in Forest, 149 (23%) originated in Shrub, 121 (19 %) originated in Moderately mixed vegetation, 80 (12%) originated in Densely mixed vegetation, and 41 (6%) originated in Sparsely mixed vegetation. Step-wise multiple regression revealed that lighting conditions ($F = 7.647$, $P = 0.006$), and the interaction of lighting conditions and initial habitat type ($F = 8.139$, $P = 0.004$) were significant but weak predictors (multiple $R^2 = 0.137$) of movement length. Night movements were longer than day movements and movement distance tended to increase at night as initial habitat quality decreased (Figure 3). During the day, however, movement distance was relatively unrelated to initial habitat quality.

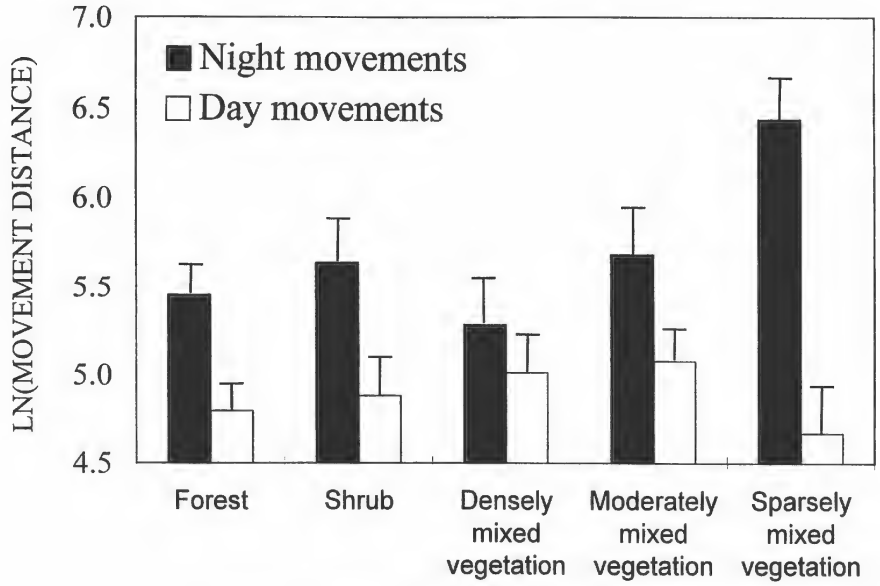

Figure 3. Mean movement distance (natural log transformed) and standard error in relation to lighting conditions (light vs. dark) and habitat type in which the movement began for coyotes in the greater Seattle metropolitan area, King County, Washington, 1989-90. Movements were represented by straight lines connecting consecutive radiolocations taken at 1-hour intervals.

Discussion

Analysis of movement data suggested that coyotes preferred relatively undisturbed habitats in urban environments of Washington State despite the fact that the amount of those habitats types (Forest and Shrub) was quite variable among home ranges and in some cases made up a small proportion of the home range (Table 1). Coyote selection for particular habitat was apparent only at the level of habitat use within the home range rather than at the level of the home range within the study area, although the failure to detect home range level habitat preference may have been an artifact of my study area description. Analysis of available habitat during movements, used habitat during movements, and to a lessor degree, habitat associated with telemetry points suggested that coyotes tended to prefer, in order of preference Forest, Shrub, Densely mixed vegetation, Moderately mixed vegetation, and Sparsely mixed vegetation (i.e., least disturbed to most disturbed). This was consistent with a previous habitat use study Quinn (1995) conducted on a temporally independent subset of the same telemetry data. Forest and Shrub probably provided the best hiding cover in urban western Washington. In addition, Shrub habitat which was typically found in transition areas between forest and more urbanized habitats may represent important foraging areas for coyotes in urban environments (Quinn 1997). Atkinson and Shackleton (1991) showed that the diet of coyotes near Vancouver, Canada, was dominated by 1 vole species (*Microtus townsendii*) found predominantly in grasslands. In this study grasslands were included in Shrub habitat.

While analysis of independent telemetry points revealed a similar but less conclusive pattern of habitat preference as movement data (also see Quinn 1995), analyzing movement data may expand the types of inferences that can be made about coyote behavior. For example data from both studies suggested that coyotes prefer relatively undisturbed habitats but movement data also suggested that coyotes remain in close proximity (within 1 hour travel time) of preferred habitat types, such as Forest and Shrub, during routine movements. Maintaining a close proximity to preferred habitats was not simply a function of home range habitat patterns since composition based on available habitat during movements was different from the composition of home ranges as a whole.

Nonrandom habitat use during movements may have been driven more by the avoidance of, than the selection for, particular habitat types. For example, Sparsely mixed vegetation had the strongest effect of all habitat types on coyote movement distance. Coyotes beginning their moves in Sparsely mixed vegetation traveled relatively long distances at night but tended to restrict movement length during the day, presumably to avoid contact with humans. In addition, few movements originated in Sparsely mixed vegetation despite the fact that this habitat typically made up a large percentage (≥10%) of coyote home ranges. Sparsely mixed vegetation, which may facilitate coyote travel at night became relatively unusable during the day. Sparsely mixed vegetation habitat is characterized by dense residential housing developments, major metropolitan areas, or industrial areas.

Heavily forested areas with low housing density provided the best daytime cover. Day movements were short possibly because they minimized the chance of being observed and/or because the best hiding habitat often occurred in small patches which limited the distance coyotes could move unobserved. Despite the fact that night movements were longer and less constrained by habitat type than day movements, urban coyotes still preferred relatively vegetated habitats at night.

Coyotes readily exploit human-derived foods (MacCracken 1982, Quinn 1997) in urban areas, which suggests that coyotes may benefit from some level of habitat disturbance even if it means limiting their movements to areas in or near undisturbed habitats. Coyotes in western Washington preferred portions of their home ranges that most resembled undisturbed habitats but persisted (or established home ranges) in urban areas with <25 % combined Forest and Shrub habitat. Thus, given the great variability in habitat compositions among coyote home ranges and the way coyotes structure their movements to stay close to hiding cover, the suitability of urban environments for coyotes may be more a function of the distribution rather than the overall quantity of preferred habitats.

I attempted to determine a general pattern of coyote habitat preference using a simple characterization of routine movements. Simplifying assumptions about animal movements will

ultimately limit the usefulness of habitat preference studies because animals tend to move at different rates of speed depending on behavior (Laundré and Keller 1981). Ideally movement data could be analyzed at multiple temporal and spatial scales, which would allow researchers to address questions about habitat preference during specific behaviors (e.g., foraging) and how different relocation time intervals affect conclusions about habitat use. Better resolution of habitat base maps and advances in technology such as the use of satellite telemetry will greatly improve our ability to examine how animal behavior is structured by the distribution and types of habitat.

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Effects of Silvicultural Treatments on Wintering Bird Communities in the Oregon Coast Range

Abstract

Changes in forest management policies in the Pacific Northwest have resulted in a broad array of management alternatives to clearcutting on state and federal forest lands. These management alternatives should be monitored for their effects on animal use, particularly during critical periods for survival. We compared abundance of resident birds among three alternative silvicultural treatments (modified clearcut, two-story, small-patch group-selection) and unharvested controls during winter. Total bird abundance was highest in small-patch stands and lowest in modified clearcuts during winter. Species richness was highest in small-patch stands and lowest in control and clearcut stands. Two species (Steller's jays [*Cyanocitta stelleri*] and golden-crowned kinglets [*Regulus satrapa*]) were most abundant in control stands and small-patch stands. Spotted towhees (*Pipilo erythrophthalmus*) were more abundant in two-story stands; dark-eyed juncos (*Junco hyemalis*) were more abundant in harvested stands than control stands. The small-patch group-selection treatment retained structural and compositional complexity of vegetation and provided habitat for more individuals than two-story or modified clearcut treatments. However, two-story and modified clearcut treatments with components of mature and old-growth forests (snags, logs, large trees) provided habitat for several bird species during winter. Silvicultural treatments that retain structural and compositional vegetation complexity or develop late-successional characteristics more quickly than stands regenerating following traditional clearcutting practices may be used by more bird species and should be considered when developing stand management guidelines.

Introduction

The availability of winter habitat may influence successful breeding and population persistence of resident bird species (Huff et al. 1991, DellaSala et al. 1996). Winter may be a more critical period for survival because of limitations or changes in seasonal food and cover resources. In fact, some species of birds exhibit morphological adaptations or behavioral characteristics that seem better adapted to survival in winter than during the breeding season (e.g., some finch species are insectivores during the breeding season but granivores during the winter and have beaks better adapted for handling seeds) (Salomonson and Balda 1977, Cody 1985).

Because bird use of habitat may vary among seasons (Cody 1985, Manuwal and Huff 1987, Hagar 1993), it is important for land managers to understand habitat needs of birds during spring breeding and winter seasons to insure adequate habitat is available (Morrison et al. 1985). Cover and food resources in late-successional forests may provide better winter habitat than early or mid-seral stages, particularly during inclement weather (DellaSala et al. 1996). Species richness and/or total abundance of diurnal birds was higher during winter in old-growth forest stands (250- to 600-year-old) than in young (42- to 75-year-old), mid-seral (65- to 140-year-old), or mature (105- to 165-year-old) stands in the Pacific Northwest (Manuwal and Huff 1987, Huff et al. 1991). In mixed-conifer forests of the Sierra Nevada, birds used areas with denser upper and mid-canopy cover in winter than during summer (Morrison et al. 1986).

The task of identifying appropriate winter and breeding habitat is complicated by changes in forest composition and structure caused by human-induced disturbances. A variety of forest management techniques (e.g., controlled burning, thinning, even-aged and uneven-aged regeneration systems) may produce very different effects on vertical and horizontal vegetation layers. Vegetation

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structure may have an important influence on bird community structure (MacArthur and MacArthur 1961, Roth 1976), so managers should understand the potential effects of disturbances on structure and resulting community composition.

Changes in forest management policies in the Pacific Northwest have resulted in consideration of a broad array of management alternatives to clearcutting on state and federal forest lands (Oregon Forest Practices Act, Forest Ecosystem Management Assessment Team 1993). Even-aged, two-aged, and uneven-aged silvicultural treatments that retain some features of old-growth forests (e.g., snags, logs, large diameter trees) but still allow some timber extraction may create stand structures that maintain habitat for birds. In a comparison of response of breeding birds to three silvicultural treatments (small-patch group-selection, two-story, and modified clearcut) and control (unharvested) stands, some bird species were most abundant in clearcut and two-story stands (e.g., white-crowned sparrow [*Zonotrichia leucophrys*], spotted towhee), while others were most abundant in uncut control or small-patch group-selection stands (e.g., brown creeper [*Certhia americana*], winter wren [*Troglodytes troglodytes*]) (Chambers 1996). Use of these stands may shift during the winter, however. If birds favor areas with greater structural and compositional complexity during the winter, they might be expected to be most abundant in control or small-patch group-selection stands, which retain all (control stands) or most (small-patch group-selection stands) of the trees and shrubs originally present in the stand (Chambers 1996). Based on this hypothesis, the objective of this study was to determine whether there were differences among resident bird use of three silvicultural treatments and control stands during winter. We used a subset of the same study sites used by Chambers (1996) so we could compare winter and breeding season habitat use by birds.

Study Area

We selected 12 stands in Oregon State University's McDonald-Dunn Forest located on the eastern edge of the Coast Range, ≤ 24 km north and northwest of Corvallis. Replicates were located near (1) Lewisburg Saddle: Township 11S, Range 5W, Willamette Baseline and Meridian (W. M.), Sections 4, 8, 9, 16, 17; (2) Peavy: Township 10S, Range 5W, W. M., Sections 25, 35, 36; and (3) Dunn: Township 10S, Range 5W, W. M., Sections 14, 22, 23, 27. Stands were 80- to 120-years old and ranged from 5 to 18 ha in size. Elevation ranged from 120 to 400 m. Douglas-fir comprised ≥ 64% basal area prior to harvest; grand fir (*Abies grandis*), bigleaf maple (*Acer macrophyllum*), Oregon white oak (*Quercus garryana*), Pacific madrone (*Arbutus menziesii*), Pacific dogwood (*Cornus nuttallii*), red alder (*Alnus rubra*), Oregon ash (*Fraxinus latifolia*), and bitter cherry (*Prunus emarginata*) comprised the remaining basal area.

Winter climate is typically wet and mild. Annual precipitation averages 100 cm; 95% occurs between October and June in the form of rain. Average annual snowfall is < 2 cm. Temperatures during January average 4.0 C (Franklin and Dyrness 1973:110-111).

The 12 stands included three replicates of four treatments: control (uncut), small-patch group-selection (1/3 volume removed in 0.2-ha circular patches), two-story (3/4 volume removed with remaining green trees [20 to 30/ha] scattered uniformly throughout the stand), and modified clearcut (1.2 green trees/ha retained). Harvesting began in fall and was completed by early spring. Lewisburg Saddle replicate was cut in 1989, Peavy replicate in 1990, and Dunn replicate in 1991. Statistical analyses were based on sample sizes of three stands per treatment.

Methods

Bird Data Collection

We sampled birds from December 1994 through March 1995, using the modified variable circular plot (VCP) method (Reynolds et al. 1980). Three VCPs were established in each stand with each VCP center at least 100 m from the stand edge and other VCP centers. We visited each VCP three times between 0900 and 1600. We alternated order of visitation among stands to account for daily variation in activity of birds. We did not conduct counts in rain or winds > 15 km/h.

Counts began two minutes after arrival at the VCP station to allow for resumption of normal bird activity. Each count lasted 15 minutes, during which time birds observed in the stand were identified to species and their approximate location mapped. We recorded distances to the nearest meter for birds ≤ 10 m from VCP station, to the nearest 5 m for birds >10 m but ≤ 50 m, and to

the nearest 10 m for birds > 50 m but ≤ 100 m. The same observer conducted all sampling.

Statistical Analyses

We compared average detection distance (m) for each species of adequate sample size (in ≥ 8 stands, ≥ 3 treatments, $n \geq 20$ observations). We used analysis of variance (SAS Institute Inc. 1989) to determine if there were differences in detection distances among treatments. Distances were transformed using a log transformation [$\log_{10}$(distance)] to meet assumptions of normal distribution and equal variance (Sabin and Stafford 1990). If detection distance did not differ among treatments, we used all observations ≤ 75 m in analyses. If we did detect differences in detection distances among treatments, we calculated 95% confidence intervals for treatment means. If the 95% confidence interval placed individuals at detection distances > 75 m, we eliminated these species from analyses.

All individuals ≤ 75 m from the VCP center were included in analyses except repeat observations of the same individual and records of birds observed flying over stands. Abundances for individual bird species were transformed using a log transformation [$\log_{10}$(bird abundance + 1)] to meet assumptions of normal distribution and equal variance (Sabin and Stafford 1990). Total abundance of all bird species and species richness were not transformed for analyses.

The experimental design was a randomized block design. We used analysis of variance (SAS Institute Inc. 1989) to determine if there were differences in average detection distances, total abundance of birds (average number of observations/stand), species richness, and individual species abundances (average number of observations/stand for species that were detected in ≥ 8 stands, ≥ 3 treatments, and with ≥ 20 total observations) among treatments. If treatment effects were significant ($P < 0.10$), we made multiple means comparisons using Scheffe's test with $\alpha = 0.10$ (SAS Institute Inc. 1989).

Results

We observed a total of 594 birds representing 30 species. Most abundant species were golden-crowned kinglet (25% of total observations), winter wren (13%), dark-eyed junco (13%), song sparrow (*Melaspiza melodia*) (7%), Hutton's vireo (*Vireo huttoni*) (6%), Steller's jay (4%), and spotted towhee (4%) (Table 1).

TABLE 1. Birds[1] observed during winter counts (December 1994 - March 1995) representing 594 observations, McDonald-Dunn Research Forest, Benton County. Silvicultural treatments are unharvested control (CN), small patch (SP), two-story (TS), and modified clearcut (CC). Species are listed in descending order of abundance.

	TREATMENT				
Common Name	CN	SP	TS	CC	TOTAL
Golden-crowned kinglet[2]	87	60	4	0	151
Winter wren[2]	26	24	15	13	78
Dark-eyed junco[2]	0	17	34	27	78
Song sparrow[2]	2	5	17	15	39
Hutton's vireo[2]	20	7	10	1	38
Steller's jay[2]	11	10	4	1	26
Spotted towhee[2]	0	4	12	8	24
Bushtit	0	20	0	0	20
American robin	1	5	5	6	17
Pine siskin	0	10	0	6	16
Evening grosbeak	0	15	0	0	15
Black-capped chickadee	7	4	2	1	14
Northern flicker	2	3	6	1	12
Red-breasted nuthatch	5	3	1	0	9
Chestnut-backed chickadee	5	2	0	0	7
European starling	0	0	0	7	7
Gray jay	3	3	0	0	6
Red-breasted sapsucker	0	2	1	3	6
Red-tailed hawk	1	1	0	4	6
American crow	0	1	4	0	5
House wren	0	0	4	1	5
Varied thrush	2	1	0	1	4
Brown creeper[2]	2	0	0	0	2
Hairy woodpecker	0	1	1	0	2
Pileated woodpecker	2	0	0	0	2
Downy woodpecker	0	0	0	1	1
Great-horned owl	0	0	0	1	1
Sharp-shinned hawk	0	0	1	0	1
White-crowned sparrow[2]	0	1	0	0	1

[1] Scientific names for species are: bushtit (*Psaltriparus minimus*); American robin (*Turdus migratorius*); pine siskin (*Carduelis pinus*); evening grosbeak (*Coccothraustes vespertinus*); black-capped chickadee (*Parus atricapillus*); northern flicker (*Colaptes auratus*); red-breasted nuthatch (*Sitta canadensis*); chestnut-backed chickadee (*Parus rufescens*); European starling (*Sturnus vulgaris*); gray jay (*Perisoreus canadensis*); red-breasted sapsucker (*Sphyrapicus ruber*); red-tailed hawk (*Buteo jamaicensis*); American crow (*Corvus brachyrhynchos*); house wren (*Troglodytes aedon*); varied thrush (*Ixoreus naevi*); hairy woodpecker (*Picoides villosus*); pileated woodpecker (*Dryocopus pileatus*); downy woodpecker (*Picoides pubescens*); great-horned owl (*Bubo virginianus*); northern pygmy-owl (*Glaucidium gnoma*); sharp-shinned hawk (*Accipiter striatus*).

[2] Scientific names are listed in the text.

Six species were observed frequently enough for statistical analyses. We did not detect a difference ($P > 0.1$) in detection distances among treatments for five of these species: golden-crowned kinglet (average distance and standard error [in brackets and indicated by '.' if sample size was too small to calculate standard error]: control [CN] 42 m [2]; small-patch group-selection [SP] 44 m [1]; two-story [TS] 60 m [.]; clearcut [CC] no observations), winter wren (CN = 31 m [7], SP = 28 [4], TS = 22 [5], CC = 24 [3]), dark-eyed junco (CN = no observations, SP = 38 [4], TS = 33 [8], CC = 20 [6]), Steller's jay (CN = 59 m [11], SP = 36 [3], TS = 55 [15], CC = 80 [.]), or spotted towhee (CN = no observations, SP = 43 [15], TS = 30 [2], CC = 25 [3]).

Song sparrow detection distance differed among treatments ($P = 0.05$). Song sparrows were recorded at closer distances in clearcuts and two-story stands. Average detection distance was 16 m (2) in clearcuts, 26 m (1) in two-story stands, 49 m (6) in small patch stands, and 60 m (.) in control stands. Differences in detection distances among treatments were likely the result of actual differences in bird use of the stands. Song sparrows usually foraged or moved among dense shrubs. Shrub patches were more evenly distributed and denser in clearcuts and two-story stands than in small patch and control stands (Chambers 1996). Probably because shrubs were too sparse (e.g., control stands) and/or patchily distributed (e.g., small patch stands), we observed only two song sparrows in control stands, and observations in small patch stands were associated with shrubs in openings. However, all song sparrow observations occurred within 75 m of the VCP center in all treatments, so we assumed that we were able to adequately detect song sparrows in all treatments.

Abundance of birds differed among treatments ($P = 0.03$) and was highest in small patch stands and lowest in modified clearcut stands (Table 2). Species richness was highest in small patch stands and lowest in control and clearcut stands ($P = 0.02$) (Table 2).

Abundance of four bird species differed among treatments ($P \leq 0.04$): Steller's jay, golden-crowned kinglet, spotted towhee, and dark-eyed junco. We did not detect differences among treatments for winter wrens and song sparrows ($P \geq 0.12$) (Table 2).

Observations of golden-crowned kinglets were most frequent in control and small patch stands compared with two-story and clearcut stands ($P = 0.0001$). Steller's jays were more abundant in control and small-patch stands and low in abundance or absent from two-story and clearcut stands ($P = 0.04$). Observations of dark-eyed juncos were higher in harvested treatments than in control stands ($P = 0.0009$). Spotted towhees were more abundant in two-story and clearcut stands, lower in abundance in small patch stands, and absent in control stands ($P = 0.002$).

TABLE 2. Abundance (observations/stand) of birds ≤ 75 m from VCP centers in 3 silvicultural treatments (small-patch group-selection, two-story, modified clearcut) and unharvested control stands averaged over 3 counts conducted between December 1994 and March 1995, McDonald-Dunn Research Forest, Oregon. Means and standard errors (SE) for total bird abundance, species richness, and individual bird species are reported as untransformed. Data for bird species were transformed using $\log_{10}$(abundance + 1) for analyses. Total bird abundance and species richness were untransformed for analyses. *P* is the probability of Type I error associated with the rejection of the null hypothesis that there is no difference among means using ANOVA (degrees of freedom = 2, 3). Means that differed significantly ($P < 0.1$) using Scheffe means separation tests are designated with different letters.

	CONTROL		SMALL PATCH		TWO-STORY		CLEARCUT		
SPECIES	Mean	SE	Mean	SE	Mean	SE	Mean	SE	*P*
Bird abundance	53.0^{AB}	5.7	65.3^{A}	6.8	38.7^{AB}	6.6	27.7^{B}	4.7	0.03
Species richness	7.7^{B}	0.3	12.3^{A}	1.4	9.0^{AB}	1.5	7.0^{B}	1.5	0.02
Steller's jay	3^{A}	1	3^{A}	1	1^{AB}	1	0^{B}	0	0.04
Winter wren	8	1	8	2	5	1	4	3	0.3
Golden-crowned kinglet	26^{A}	2	20^{A}	3	1^{B}	1	0^{B}	0	0.0001
Spotted towhee	0^{C}	0	1^{BC}	0	4^{A}	1	3^{AB}	1	0.002
Song sparrow	0.3	0.3	2	1	6	2	5	3	0.12
Dark-eyed junco	0^{B}	0	6^{A}	1	11^{A}	4	9^{A}	3	0.0009

Discussion

Many species of birds alter their use of habitat between seasons because of changes in habitat structural features that affect availability of cover and roost sites (Morrison et al. 1986, Huff et al. 1991). Quantity and quality of food resources also may vary seasonally, and birds may alter foraging locations or patterns to obtain food (Martin et al. 1951, Conner 1980, Hutto 1981, Lewke 1982, Morrison et al. 1985).

Following harvest, abundance of breeding birds was higher in control (uncut) and small-patch group-selection stands than in two-story and clearcut stands (Chambers 1996). Bird communities in control and small-patch stands were dominated by migratory bird species whereas resident bird species were more abundant in two-story and clearcut stands (Chambers 1996). During the winter season, resident birds were more abundant in stands with higher canopy cover and least abundant in clearcut stands, although differences among control and two-story treatments were not statistically different from small-patch and clearcut stands.

Two species associated with forests (golden-crowned kinglet and Steller's jay) were low in abundance or absent from clearcut stands. Steller's jays were more abundant in control and small patch stands, lower in two-story stands and almost absent in clearcut stands; these patterns were the same as those observed during the breeding season (Chambers 1996) so it seemed that Steller's jays did not alter use of habitat seasonally.

Golden-crowned kinglets were most abundant in control and small-patch stands. This pattern was similar to the pattern observed during the breeding season (Chambers 1996). Morrison et al. (1986) also found no difference between habitat use of golden-crowned kinglets during winter and summer in a mixed-conifer forest in Sierra Nevada, California. Marcot (1985) and Huff et al. (1991), however, did find a seasonal shift in habitat use by golden-crowned kinglets in Douglas-fir forests in the Pacific Northwest. Marcot (1985) found golden-crowned kinglets were more abundant in sawtimber stands during breeding season, but during the rest of the year their density was highest in shrub-sapling stages. Huff et al. (1991) found kinglets more abundant in mid- than late-seral stands during the winter. The two-story and clearcut stands we studied were recently harvested (within the previous five years) and were structurally simpler than control and small patch stands (Chambers 1996). Conditions in these stands may not have provided adequate cover or food for kinglets.

We did not detect a treatment response for winter wrens, a forest-associate that is sensitive to forest fragmentation (Rosenberg and Raphael 1986, Lehmkuhl and Ruggiero 1991, McGarigal 1993). However, winter wrens were more abundant in control and small-patch stands than in two-story and clearcut stands during the breeding season (Chambers 1996). This may indicate a seasonal shift in habitat use. It also may indicate that dispersing juveniles use poorer quality habitat in winter (e.g., clearcuts and two-story stands) because better sites are already occupied by adults (Van Horne 1983). In California, Barrows (1986) found winter wrens occurred almost exclusively in old-growth forests during the breeding season, but were more randomly distributed among stands of different seral stages in winter. Winter wrens may be more selective of habitat for breeding sites than for winter use.

Spotted towhee abundance was significantly higher in heavily disturbed areas (modified clearcut and two-story stands) than lightly disturbed (small-patch group-selection) or control stands during the breeding season (Chambers 1996). The pattern of habitat use in winter was similar. We observed spotted towhees most frequently in clearcuts and two-story stands. They were also present in small-patch stands but we did not observe them in control stands. Spotted towhees did not appear to alter their use of habitat during the year.

During the winter, dark-eyed juncos were more abundant in clearcut, two-story, and small patch stands than in control stands. However, Chambers (1996) found dark-eyed juncos abundant in all stand types (including control stands) during the breeding season. They seemed more selective of winter habitat, using areas with more disturbance.

No difference in song sparrow abundance was detected among treatments during the winter season. Chambers (1996) did not have an adequate sample size during the breeding season to test for treatment differences.

Cody (1985) suggested that in the winter, birds may occupy niches vacated by migratory or summer visitors. We did detect seasonal shifts for some species. During the winter, some species became

more selective (e.g., dark-eyed junco), some maintained the same degree of selectiveness (e.g., golden-crowned kinglet, spotted towhee), others became less selective (e.g., winter wren). Species such as the winter wren may occupy niches vacated by migratory species. Change in habitat use also might be attributed to occupation by dispersing juveniles Juveniles may use poorer quality habitat (e.g., clearcuts) because better habitat is already occupied by adults. We did not find a change in seasonal use of habitat for most of the species in our study.

Manuwal and Huff (1987), Morrison et al. (1986), and Huff et al. (1991) have suggested that structural features of late-successional forests and forests with dense upper- and mid-story canopies offer better habitat to resident birds during winter. Although we did not find greater use of mature forest (control stands), total bird abundance was higher in small-patch stands. These stands retained significantly higher canopy cover in the overstory (sawtimber cover, > 20 m) than two-story or modified clearcut stands (Chambers 1996). Our data indicate a need for a variety of seral stages on a landscape to provide habitat for all winter resident bird species, but stands that are more similar to mature forest may provide habitat for higher numbers of individuals.

Total winter bird abundance was approximately 1.5 times higher in control, small patch, and two-story stands than in clearcut stands. In other Pacific Northwest studies, birds were more abundant in late-successional stands than in younger forest seral stages (Manuwal and Huff 1987, Huff et al. 1991). Retaining late-successional forest stands or structural features (e.g., large diameter green trees) may be particularly important in areas being managed under short (40 to 80 year) rotations and planted with a single tree species since structure and composition may be much simpler than late-successional forests. Habitat selected by some birds may never develop under these management conditions (Morrison et al. 1986). However, in this study, some bird species (spotted towhee and dark-eyed junco) were more abundant in clearcuts and two-story stands. We suggest maintaining a variety of seral stages or structural conditions to provide habitat for species associated with early seral stages.

Although stand conditions in two-story and clearcut treatments in our study did not provide mature forest structure, they retained or created some elements (snags, logs, large trees) of old-growth forests and added to stand-level structural complexity. For winter birds that use late-successional forests, these features may provide habitat earlier in stand development than traditional clearcuts. Treatments that develop late-successional characteristics more quickly or retain structural and compositional complexity may be used by more bird species and should be considered when developing stand prescriptions.

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Bilateral Asymmetry, Sexual Dimorphism, and Nematode Parasites in Mature Male Sockeye Salmon *Oncorhynchus nerka*

Abstract

The extent of bilateral asymmetry of 310 mature male sockeye salmon (*Oncorhynchus nerka*) from 6 Alaskan populations was determined to investigate the relationship between fluctuating asymmetry in paired morphological characters and physical traits (body size and shape) that seem to signal male quality. There was marked variation within and among populations in body size and morphology (e.g., body depth), but no differences in the overall level of asymmetry were detected among the populations, nor between the two systems investigated (lakes Aleknagik and Iliamna). The counts or measurements of a number of the traits evaluated for asymmetry varied among populations, but most differences were attributable to population-specific variation in body size. The six populations exhibited marked similarities in the patterns of asymmetry. Three paired characters (length of pectoral fins, number of branchiostegals, and number of teeth) were directionally asymmetric, indicating a genetic basis for asymmetry rather than an environmental influence. Two other paired characters (ventral fin length and number of enlarged teeth) were bilaterally variable but not correlated with any attribute of male quality.

Based on the low variation between the different populations in level of asymmetry, we conclude that either stress does not influence asymmetry levels in sockeye salmon or that these populations are under similarly low levels of stress.

We also explored the relationship between biomass of a nematode parasite (*Philonema oncorhynchi*) and asymmetry. The weight of parasites was related to fluctuating asymmetry in the ventral fin length but was not related to fluctuating asymmetry in number of large teeth.

Introduction

There is an ever increasing demand for better understanding of biological diversity and its assessment and maintainance. In plants and animals bilaterally symmetric morphological characters demonstrate fluctuating asymmetry when symmetry is the rule and there is no tendency for the trait value of one side to be larger than that on the other side. The determination that bilateral symmetry is related to the developmental stability has provided a way to assess environmental impacts on the individual developmental programs in biological systems, complementing data from genetic surveys (Sarre et al. 1994; Alados et al. 1995; Wagner 1996; Møller 1996).

Deviations from bilateral asymmetry are common and are usually characterized by a frequency distribution of right (R) minus left (L) measurements (e.g. Palmer and Strobeck 1986). The three currently accepted forms of bilateral asymmetry are fluctuating asymmetry, characterized by a normal distribution of the individual R-L values with a mean of zero, directional asymmetry, characterized with a mean significantly different from zero and antisymmetry, which arises as a genetic predisposition of an individual towards asymmetry, but without a specific bias to left or right. In the last case, the mean deviation of the individual R-L is zero, but the distribution is platykurtic (Palmer and Strobeck 1986; Palmer 1996).

Asymmetric features may have a negative effect on behavioral patterns associated with reproduction (e.g., Møller 1992a; Balmford and Thomas 1992; Balmford et al. 1993) thus reducing reproductive success, and asymmetry appears to have low heritability and appears largely to be caused by disruption of developmental processes (Clarke 1995).

Semelparous Pacific salmon (*Oncorhynchus* spp.) have a number of life history traits which make them favorable for tests of hypotheses of sexual dimorphism and mate choice. The lifetime

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reproductive effort of individuals takes place over about 2-3 weeks at population- specific spawning sites. Maturation leads inevitably to death; postponement of resources to future reproduction is thus impossible. Salmon develop dramatic secondary sexual characters at maturity. The most conspicuous features are the extended snout with large teeth and the exaggerated dorsal hump of males. The salmon must invest energy to develop these features, and they may thus signal the male's energetic status or other indices of quality. These secondary sexual features are developed late in the life cycle with the limited energy resources acquired at sea and in conflict with other energetic demands as migration and gonad development. The extent of development of these features also varies among genetically distinct populations within species (Beacham 1985; Beacham and Murray 1987; Beacham et al. 1988; Blair et al. 1993).

Quinn and Foote (1994) reported that the size of certain sexually dimorphic features (body depth and, to a lesser extent, jaw length) was positively correlated with male social status and access to females, independent of body length in sockeye salmon *O. nerka* Walbaum. Body depth was closely correlated with condition factor (weight/length ratio) and the dorsal hump seems to be used in male-male displays. Jaw size, also correlated with condition factor, affects the male's ability to gape over a competitor, and thus the effectiveness of the jaws as a weapon. The development of the secondary sexual characteristics is rapid and takes place just prior to the spawning period. Fish with pronounced secondary characteristics may therefore either have a relatively large index of asymmetry due to inappropriate developmental resources or a relatively low value if indicators of sexual quality such as the size of sexual characteristics and level of asymmetry are correlated. No specific relationship between the size of secondary sexual characteristics and level of asymmetry can thus be predicted.

Hamilton and Zuk (1982) hypothesized that there is a negative correlation between parasite load and secondary sexual characteristics. No correlation was detected between the size of the secondary sexual characteristics of sockeye salmon and weight of the dominant parasite, a nematode *Philonema oncorhynchi* Kuitunen-Ekbaum in several Alaskan populations (Berg et al. 1995). However, the interrelationships between parasites, asymmetry and secondary sexual characteristics were not explored. The purpose of this study was to assess the amount of asymmetry, primarily fluctuating asymmetry, of a number of populations of sockeye salmon from a relatively unpolluted and pristine area and correlate the asymmetry with parasite load and accepted predictors of male social status.

Methods

We compared indicators of male quality (the length of the male and the extent of development of secondary sexual characteristics), with the degree of asymmetry in several morphological traits in 310 male sockeye salmon from two oligotrophic Alaskan lakes, Lake Aleknagik and Iliamna Lake (Fig. 1). We also compared the degree of asymmetry with parasite load in 255 of the fish (Berg et al. 1995). The sockeye salmon in these lakes were selected for study because there is a large amount of information on the populations, including age structure (Rogers 1987; Blair et al. 1993), morphology (Bishop 1990; Wetzel 1993; Blair et al. 1993) and spawning behavior (Quinn and Foote 1994; Quinn et al. 1996). The study populations are very abundant and productive, and are not on the periphery of the species' range, and therefore were probably not under extreme environmental stress.

The fish were collected immediately before spawning with beach seines or gill nets on or near their spawning grounds between July 25 and August 20, 1993. Sockeye salmon from two small creeks draining into Lake Aleknagik, Yako Creek and Happy Creek, were collected as they schooled just outside the creek mouths. Sockeye from Hansen Creek, also on Lake Aleknagik, were largely sampled among sockeye killed by brown bears *Ursus arctos* L., but not eaten. In Iliamna Lake, samples were collected at Finn Bay, Knutson Bay, and Woody Island (for details see Berg et al. 1995). We attempted to sample the salmon at the peak of their development of secondary sexual characteristics (Quinn and Blair 1992) but the Finn Bay fish were not fully mature in comparison to the other Iliamna Lake populations. Fish were processed as quickly as possible after capture.

The size or count of several bilateral characters was recorded to indicate asymmetry. The number of branchiostegals (rays attached anteriorly to the hyoid bones, ventral to the gill cover)

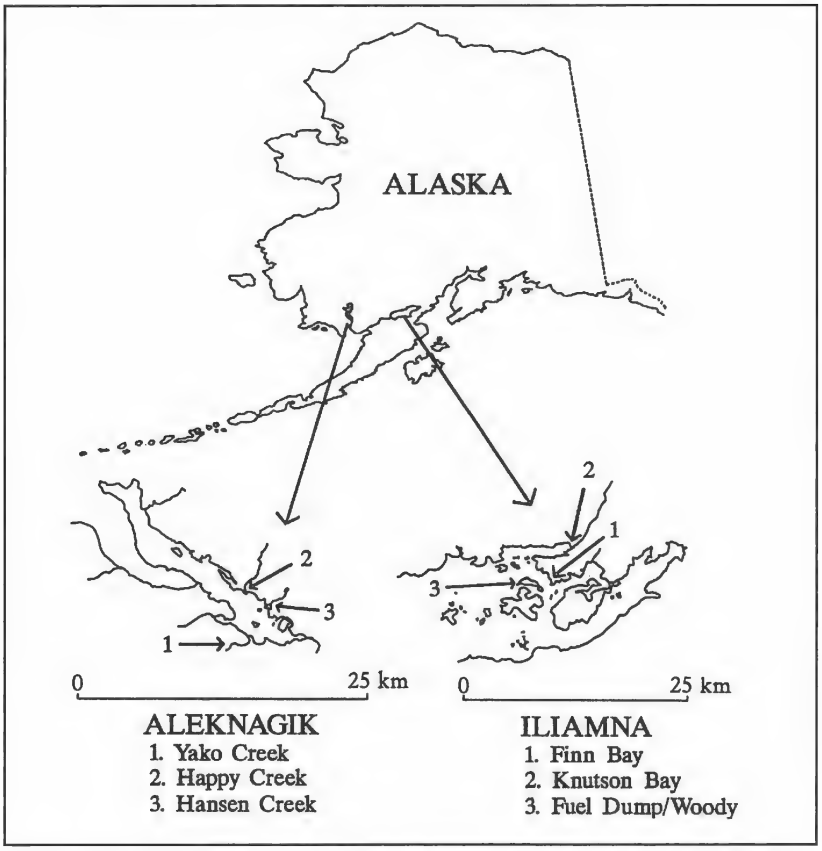

Figure 1. Map of Alaska, showing the sampling locations.

is apparently set early in life (Gharrett and Smoker 1991), and these were counted on both sides. We also measured several characters whose size or number is more likely to be affected by environmental conditions throughout development, including pectoral and ventral fin lengths, and the number of teeth on the upper and lower jaws. The length of each pectoral fin was measured with calipers as the distance (in mm) between the outer margin of the pectoral fin and the distant edge between the base of the fin and scapula (shoulder bone). The length of each ventral fin was determined between the outer margin of the fin along the inner edge to the papilla at the base of the fin. In the upper jaw there was a distinct gap in dentition about one-third of the way along the jaw from the front. The number of teeth was determined in this well-defined anterior area. These upper jaw, frontal teeth should be of importance for fighting capacity of males. We also counted the number of large teeth (> 3 mm). The enlargement of some teeth is a secondary sexual characteristic developed just prior to spawning.

Asymmetry of a character was calculated as the absolute difference in the length (or count) of the character between the right (R) and left (L) sides. R-L distributions that depart significantly from the statistical criteria for ideal fluctuating asymmetry (mean of zero, normal distribution) are unsuitable as descriptors of developmental stability because a part of the asymmetry variation may have a genetic basis (Palmer and Strobeck 1992). Three characters (pectoral fin length, number of branchiostegals, total number of teeth) exhibited significant directional asymmetry and were therefore not utilized as indices of fluctuating

asymmetry (Palmer and Strobeck 1992). Two other characters (ventral fin length, number of big teeth) showed no directional asymmetry or antisymmetry, and were used to characterize fluctuating asymmetry. Seven extreme observations out of a total of 4,960 (310 fish x 16 morphological measurements) were discarded, as they were thought to be either recording errors or physical deformities unrelated to fluctuating asymmetry.

We selected several morphological features for measurement on the basis of their involvement in male displays, aggression, and social status (Quinn and Foote 1994). These included length (from the middle of the eye to the end of the hypural plate), and three secondary sexual characteristics: body depth (perpendicular to the long axis of the fish from the anterior insertion of the dorsal fin to the belly), snout length (mid-eye to tip of upper jaw), consistent with Quinn and Blair (1992) and Quinn and Foote (1994), and the number of large teeth. As all three secondary sexual characteristics were correlated with fish length, we substituted the residuals of site-specific regressions of these characters on body length for their raw values (Quinn and Foote 1994).

Parasite load was measured as the wet weight of the dominant macroparasite in these populations, the nematode *Philonema oncorhynchi*. Parasites within the abdomen were readily visible and easily collected for later assessment (Berg et al. 1995). The distribution of parasite weights was highly skewed, accordingly, the natural logarithm of parasite load was used for all analyses. Only 1 of 255 fish assessed for parasites had none, to permit log transformation, the smallest observed parasite load was substituted for this observation. We calculated all possible correlations between the four signals of male quality (length and the residuals of the three secondary sexual characteristics) and the hypothesized predictors of male quality (fluctuating asymmetry and parasite load). We also calculated the correlations between parasite load and the degree of fluctuating asymmetry.

Results

There was marked variation within and between sites in the size of morphometric or number of meristic traits (Table 1). Continuous characters (body depth, snout length, fin lengths) were strongly positively correlated with body length ($p < 0.001$). The number of small and large teeth in the upper jaw was significantly correlated with length ($p < 0.001$). The numbers of lower jaw teeth count had correlations with length with p ranging between 0.15 (not significant) and 0.01 among the populations. Branchiostegal number was not correlated with body length. The populations differed in mean length and many of the inter-population differences disappeared when fish length was accounted for. Analysis substituting sea age (where most growth occurs) for body length yielded similar patterns of correlation and of statistical significance. Nevertheless, some traits varied between Lake Aleknagik and Iliamna Lake, notably body depth even after the effects of size were removed ($p < 0.05$).

There were a number of inter-trait correlations between the different characters within the pooled material such as between number of upper (and lower) jaw teeth and both pectoral and ventral fin

TABLE 1. Pooled (common) mean length/count of the different characters from the different sites. Fish, pectoral and ventral fin lengths are in mm, while other characters are counts.

	Length of fish	Pectoral fin length	Ventral fin length	Branchio-stegals	Upper big teeth	Upper total teeth	Lower big teeth	Lower total teeth	Sample size*
Yako	449	83.8	61.3	13.2	2.7	7.6	3.4	17.6	50
Happy	468	89.4	63.9	13.1	3.2	7.8	3.7	18.5	52
Hansen	449	82.7		11.9	3.2	7.7	3.3		55
Aleknagik	**455**	**85.3**	**62.7**	**12.7**	**3.0**	**7.7**	**3.5**	**18.1**	**157**
Finn Bay	462	88.1	63.8	12.3	3.1	7.1	3.8	19.4	32
Knudson	498	96.2	68.9	12.6	3.3	7.7	3.5	17.5	60
Fuel Dump	459	88.7	66.6	13.2	3.0	7.1	3.6	17.7	61
Iliamna	**475**	**91.8**	**67.1**	**12.8**	**3.1**	**7.4**	**3.6**	**17.8**	**153**

* maximums—not all measurements were obtained for every fish

TABLE 2. Pooled (common) mean difference (right—left side) for measured bilateral characters in the different populations

	Pectoral fin length	Ventral fin length	Branchio-stegals	Big teeth	Total teeth
Yako	-2.4	-1.0	-0.9	-0.1	0.1
Happy	-1.7	-0.2	-0.6	0.2	0.4
Hansen	-0.4		-0.8	-0.2	
Aleknagik	**-1.5**	**-0.6**	**-0.8**	**0.0**	**0.2**
Finn Bay	-0.5	-1.0	-1.5	0.3	0.5
Knudson	-0.5	-0.1	-1.4	0.0	1.2
Fuel Dump	-0.8	0.5	-1.2	0.4	1.2
Iliamna	**-0.6**	**0.0**	**-1.3**	**0.2**	**1.1**
All	**-1.1***	**-0.2**	**-1.0***	**0.1**	**0.7***

* mean differs significantly from 0 (Mann-Whitney U test, $p < 0.05$)

size ($p < 0.05$). Three paired characters were directionally asymmetric (Table 2) implying a partial genetic basis to the asymmetry rather than pure environmental influences (Palmer and Strobeck 1992). Pectoral fin length and the number of branchiostegals were greater ($p < 0.0001$, Mann-Whitney U-test) on the left than on the right side, whereas the total number of teeth was greater ($p < 0.002$, Mann-Whitney U-test) on the right side. Ventral fin length and number of large teeth were thus the two characters left where fluctuating asymmetry could be detected and the six populations exhibited similar patterns of asymmetry in the measured traits.

Fluctuating asymmetry in ventral fin length was weakly but significantly ($p < 0.02$) negatively correlated with the length of male sockeye (Table 3) and a similar but positive correlation ($p < 0.02$) was found between another index of condition, residual body depth, and fluctuating asymmetry in the number of large teeth. Other correlations between indices of condition and the degree of asymmetry varied in sign, but were not significant, though there was a nearly significant negative relationship between the number of large teeth and the aysmmetry in their counts ($p < 0.06$). Overall, there was no consistent pattern of correlations between signals of male quality and fluctuating asymmetry. There were no correlations ($p > 0.05$) between the logarithm of parasite *Philonema oncorhynchi* weight and the four indices of male condition (Table 3). Parasite load was related to fluctuating asymmetry in the ventral fin length ($p < 0.05$, $r = 0.17$) but was not related to fluctuating asymmetry in number of large teeth ($p > 0.05$, $r = 0.08$).

TABLE 3. Correlation (r) between indices of male quality and fluctuating asymmetry or parasite load

Indices of male quality	FA in ventral length	FA in # big teeth	ln (Parasite) load)
Length	-0.13*	0.01	-0.04
Residual Hump	0.02	0.13*	0.07
Residual Snout	0.08	-0.03	-0.03
Residual # Big Teeth	0.04	-0.12	0.01

* = $p<0.05$

Discussion

Fluctuating asymmetry is considered to be an epigenetic measure of the ability of individuals to undergo identical development of a bilaterally symmetrical character. The present study was designated to get a reliable estimate of fluctuating asymmetry in a number of characters. A large number of measurements (nearly 5000) should provide a basis for a discussion of asymmetries among the selected populations. Several authors agree that antisymmetry and directional asymmetry may have a partial genetic basis, rendering these forms of asymmetry useless for studies of developmental instability (see e.g. Palmer & Strobeck 1986; Graham et al. 1993). Of five characters investigated, three were directionally asymmetric. Such parameters are not used in the statistical basis for fluctuating asymmetries, as the difference between sides probably reflect more than simple developmental noise (e.g. Palmer 1996). Further comparisons among populations of sockeye at more marginal areas of their range should be performed with a wider character set, where other (fluctuating) asymmetric characters could be included.

The body length, weight and particularly body depth varied between the populations from Lake Aleknagik and Iliamna Lake. Such an effect may be explained by the fact that the Alekgnagik populations we sampled were creek-spawners, whereas the populations sampled from Iliamna Lake spawn on beaches. The limited access to shallow creeks by deep-bodied males and size-selection predation by bears (Hanson 1992) have been hypothesized to influence population-specific patterns of size and morphology (Rogers 1987; Blair et al. 1993; Quinn and Foote 1994).

Substituting sea age for body length did not alter the significant correlations nor the interaction between the factors. The results were therefore given as relationships with body size and not with the factor sea age which is intercorrelated with size.

Genetic surveys of natural populations may be insufficient to identify populations with genetic problems or to detect the impact of environmental stress on the population. The possibility that a morphological approach using the frequency and size of asymmetries can complement the biochemical techniques for assessing components of adaption of natural populations (e.g. Sarre et al. 1994) is very attractive. A rapidly growing literature indicates a correlation between developmental instability and asymmetry, implying that asymmetry might also be used as an indicator of environmental stress (e.g. Soule 1967; Palmer and Strobeck 1986; Parsons 1990; Møller 1992a,b; Emlen et al. 1993), although some authors have cautioned about comparisons between taxonomic groups (Clarke 1997) or to the widespread use of fluctuating asymmetry in a variety of comparisons (Palmer 1996). The populations that we investigated showed similar levels of asymmetry. We conclude that either stress does not influence asymmetry in sockeye salmon or these populations are under similar levels of stress.

The question of honest signalling (i.e., whether individually variable traits reflect indices of fitness like condition, energetic content or parasite infection load of the animal) in mate choice situations has been treated in a number of investigations (e.g. Balmford et al. 1993; Evans 1993; Møller and Pomiankowski 1993; Evans et al. 1995; Folstad et al. 1996). Most studies have shown positive correlations between presumably beneficial physical characters and reproductive success, but few experimental studies have been performed. Wiley (1991) reviewed some of the experimental studies and concluded that behavior patterns rather than morphology might explain differences in reproductive sucess.

Quinn and Foote (1994) found that body length and especially body depth of Woody Island male sockeye salmon were associated with spawning ground status and reproductive opportunity. The fitness of an individual is affected by many factors, and the size of morphological traits and levels of asymmetry may correlate with fitness. Fitness is, however, also influenced by vigor and fish with relatively large investments in secondary characters may have less energy left for the demanding reproductive behavior patterns. Some of the morphological characters, notably teeth counts, are developed at a late stage, when the other secondary sexual characteristics are also developed. The development of these features may stress the fish, thus increasing asymmetry. Enlargement of the frontal teeth into secondary sexual characteristics occurs at what could be a stressful period in the life cycle, when salmon are migrating from saltwater to freshwater, undergoing major environmental, physiological and morphological changes. Body depth becomes exaggerated at this time and deep-bodied males had less symmetrical counts of large teeth than small males. However, Clarke (1995) reviewed the evidence and concluded that there was inadequate evidence to support any application of fluctuating asymmetry as a fitness measurement. He further questioned whether fluctuating asymmetry should be used as a substitute for conventional fitness measurements within conservation programmes. Our results are consistent with those conclusions.

Parasite load and the degree of fluctuating asymmetry in ventral fin length were significantly correlated, but not with asymmerty in the number of large teeth. The parasites were acquired by juvenile salmon while they are rearing in freshwater prior to seaward migration (Berg et al. 1995). There was no relationship between parasite load and indices of male condition. Correlations were weak and sometimes even positive, despite a wide range in parasite loads (0—28 g: Berg et al. 1995). The maximum weight of parasites observed (28 g) was less than 1% of the weight of the average salmon, however, these loads constituted a large fraction

of the space available in the body cavity, obscuring many of the organs. Parasite weight of *Philonema oncorhynchi* is not a useful indicator of stress during the buildup of the secondary sexual characteristics of the salmon.

Studies have reported positive and negative evidence for relationships between parasite load or fluctuating asymmetry and indices of fitness (Holmes and Zohar 1990; Folstad and Karter 1992; Alados et al. 1995; Folstad et al. 1996; review by Møller 1996) and meta-analysis has indicated considerable variation in support for such hypotheses (e.g., Hamilton and Poulin 1997) . The absence of correlations in our study may contribute to an assessment of the overall prevalence of such phenomena as they provide a balance to the "positive" results that are more readily published. We conclude with Csada et al. (1996) and Palmer (1996) that it is important to report results such as ours that do not conform to current research trends.

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Movements of Bull Trout (*Salvelinus confluentus*) in the Clark Fork River System after Transport Upstream of Milltown Dam

Abstract

Populations of bull trout in the Clark Fork River drainage of western Montana are small and fragmented by hydroelectric dams. The movements of four adult bull trout in this river were monitored by radiotelemetry after transport upstream of Milltown Dam. Two fish migrated 40 and 130 km to tributary streams of Rock Creek; one of these likely spawned. Two other bull trout moved downstream of the dam and appeared to later attempt to re-ascend. Movements of these bull trout suggest that Milltown Dam blocks migrations and that transporting fish upstream of the dam can enhance populations. Given the small sizes of bull trout populations in the Clark Fork River drainage, the benefits derived from transporting adult fish over dams is potentially great.

Hydroelectric dams have negative impacts on migratory fish populations. Direct impacts include mortality from turbine entrainment, gas bubble trauma, and columnaris disease (Fujihara and Hungate 1971, Marcey et al. 1978). Dams also eliminate or restrict upstream migration of adults, affecting the ability of fish to reproduce in their natal environment (Gray and Haynes 1980, Cada and Sale 1993) and metapopulation dynamics (Rieman and McIntyre 1995). These impacts have been mitigated in many river systems with anadromous fish by passage facilities, but have been largely ignored in systems with only potamodromous fish. For example, dams in western Montana are not required by the Federal Energy Regulatory Commission to provide upstream passage, although many rivers and lakes in the region contain bull trout *Salvelinus confluentus*. This species is known to make migrations in excess of 200 km (Bjornn and Mallet 1964, Shepard et al. 1984).

Many populations of bull trout are declining (Rieman and McIntyre 1993), in part due to hydroelectric dams (Fraley and Shepard 1989, Rode 1990, Bond 1992). While detrimental to all life history forms, dams particularly affect fluvial, or river-dwelling, bull trout. This fish historically moved throughout the Clark Fork River system of western Montana (Montana Bull Trout Scientific Group 1996), but with the construction of four dams between 1902 and 1952, upstream movement has been largely eliminated. Because bull trout populations in the Clark Fork River drainage are now small and uncommon (Peters 1985), transporting adult fish upstream of dams may restore historic connectivity and significantly enhance upstream populations. To evaluate the effectiveness of this action, bull trout were transported upstream of Milltown Dam, and radiotelemetry was used to monitor movements.

Study Area

Milltown Dam, a five-turbine hydroelectric facility constructed in 1907, is located at the confluence of the Clark Fork and Blackfoot rivers (Figure 1). It is operated as a run-of-the-river facility, with a 6-ha storage reservoir, a vertical spillway drop of 12 m and an average annual discharge of 86 m^3/s. It is a barrier to the upstream passage of fish.

The origins of bull trout in the Clark Fork River immediately downstream of Milltown Dam are not well understood. Because other dams on the lower Clark Fork River block upstream passage, possible natal areas downstream of the dam exist in only six streams; a single fluvial redd was documented in one of these streams in 1994 (Montana Department of Fish, Wildlife and Parks, unpublished data). In contrast, 160 and 198 bull trout redds were counted in the Rock Creek and the Blackfoot River drainages, respectively, in 1996 (Peters et al. 1997, Beaverhead-Deerlodge National Forest, unpublished data); both drainages are upstream of Milltown Dam (Figure 1). Bull

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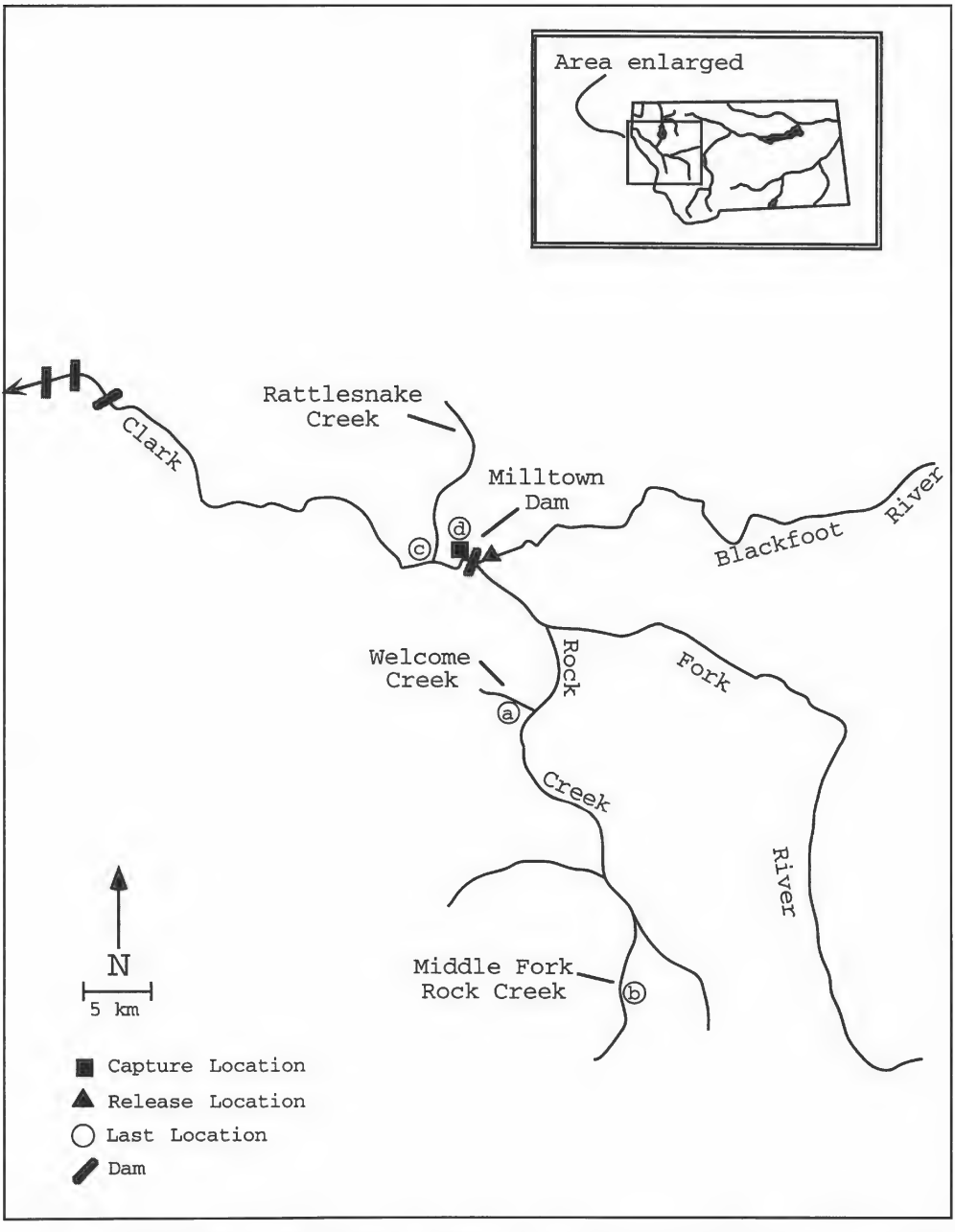

Figure 1. Clark Fork River drainage of western Montana, showing locations bull trout were captured, released and last located. Letters for final locations correspond to fish listed in Table 1.

TABLE 1. Summary of telemetry data. For capture method, HL = hook-and-line and ES = electroshock.

Fish	Length (mm)	Weight (g)	Date Captured	Capture Method	Days Tracked	Number of Contacts	Final Location
a	508	1080	18 May 94	HL	146	11	Welcome Creek
b	505	1240	16 May 94	HL	236	15	Middle Fork Rock Creek
c	642	3015	25 May 94	ES	220	30	downstream Milltown Dam
d	725	4876	25 May 94	ES	680	4	downstream Milltown Dam

trout immediately downstream of Milltown Dam likely originated from these drainages.

Welcome Creek is a small, second-order tributary to lower Rock Creek. Although juvenile bull trout occur here, no fluvial adults have been observed (Montana Department of Fish, Wildlife and Parks, unpublished data). The Middle Fork of Rock Creek, a third-order stream, is one of the primary spawning areas for fluvial bull trout in the drainage; 24 redds were counted there in 1994 (Beaverhead-Deerlodge National Forest, unpublished data).

Methods

Four bull trout were captured in the spillway pool downstream of Milltown Dam (two by hook and line and two by electroshocking) between 9 and 25 May 1994. After capture, fish were anesthetized (150 mg/L tricaine, MS-222), measured (total length), weighed, and transmitters surgically implanted (Swanberg 1997). Surgeries lasted 5 to 14 minutes (mean: seven minutes), during which time gills were bathed with diluted MS-222 to maintain unconsciousness. After surgery, fish were transported to the lower Blackfoot River, 200 m upstream of Milltown Dam. Locations of fish were detected from the ground using radial truck-top and three-element Yagi antennas. During periods of upriver migration, monthly flights were conducted 100 to 200 m over the river at 100 km/h with a three-element Yagi antenna attached to a wing strut. Transmitters emitted signals at 150 MHz, weighed 16 g and did not exceed 2% of fish weight, as suggested by Winter (1996). Fish were relocated at least once monthly from 9 May 1994 to 15 April 1996.

Results

Bull trout receiving transmitters ranged in length from 505 to 725 mm (Table 1). Transmitters were active from 146 to 680 d (Table 1). Two bull trout (fish a and b) moved into Rock Creek immediately after release. One of these trout (fish a) migrated 40 km in 23 d, entering Welcome Creek on approximately 17 July (Figure 1). This fish dropped its transmitter sometime after 4 August. The second bull trout in Rock Creek (fish b) migrated 130 km in 78 d, entering the Middle Fork of Rock Creek on 26 July (Figure 1). This fish was last located two weeks before the spawning period in the spawning area; it likely spawned.

A third bull trout (fish c) moved downstream of Milltown Dam on 8 June and descended 10 km to the Rattlesnake Creek confluence (Figure 1). After 65 d at this location, it wandered for 11 d. During this time, 5 km of the Clark Fork River were ascended, descended, and 3 km of Rattlesnake Creek ascended. After less than 3 d in Rattlesnake Creek, the fish ascended 10 km of the Clark Fork River to the base of Milltown Dam, where it remained for 38 d before again descending to the vicinity of Rattlesnake Creek on 20 October.

The fourth bull trout (fish d) was located upstream of Milltown Dam three times immediately after release. After 3 June 1994 this fish was not located for two years, although during this period much of the study area was searched by plane. On 10 April 1996 it reappeared at the base of the dam. Evidently it too moved downstream of the dam, perhaps to a deep pool where the transmitter signal attenuated before reaching the water surface.

Discussion

Conclusions from a sample size of four must be conservative. The number of fish tracked is, unfortunately, a reflection of the density of bull trout in the Clark Fork River. Nevertheless, implications exist for managing the passage of bull trout at dams.

Two of the four bull trout that were moved upstream of Milltown Dam entered spawning tributaries, and at least one apparently spawned. It is likely these fish returned to their natal stream because, similar to other salmonids, bull trout are thought to have strong fidelity to natal streams (Goetz 1989). No fluvial bull trout had been previously observed in Welcome Creek, although they have been seen in similarly sized tributaries to Rock Creek (Montana Department of Fish, Wildlife, and Parks, unpublished data). Due to the small size of this stream, the number of bull trout in it is probably small. If the fish entering this stream spawned, it likely made a significant contribution to the population. The movements of these two bull trout suggest that transport upstream of Milltown Dam can enhance populations. Fernet and O'Neil (1997) noted similar success for bull trout transported upstream of a newly constructed dam in Alberta, Canada.

The movements of fish c and d to the base of Milltown Dam suggest that Milltown Dam blocked further upstream movement. In a study of the movements of bull trout in the Blackfoot River, Swanberg (1997) documented three fish (mean size 580 mm) moving downstream of Milltown Dam. This result, combined with data from this study, suggest that bull trout would use the Clark Fork River drainage as a migratory system if passage existed at Milltown Dam.

Transporting fish upstream of dams is labor intensive (Cada and Sale 1993). However, the small number of bull trout likely to be encountered in the Clark Fork River makes the effort feasible and the most economical alternative for fish passage. Furthermore, because most tributaries to the Clark Fork River have a small number of spawning bull trout, enhancement by just one adult fish can contribute significantly to recruitment. Lastly, the recovery and conservation of bull trout populations ultimately requires an increase in the number of reproducing fish. Other conservation techniques (e.g., increasing spawning or rearing habitat, removing non-native species) may indirectly increase numbers of reproducing bull trout over time. In contrast, transporting adult bull trout upstream of Milltown Dam, as well as other dams in the region, is one recovery method that would have an immediate and direct response.

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Soil Development on a Pleistocene Terrace Sequence, Boise Valley, Idaho

Abstract

Study of a sequence of terraces in the western Snake River Plain of Idaho reveals a record of at least seven terraces, the ages of which span the Pleistocene. In the Boise Valley, the youngest terraces are less than ~14,500 yr and the oldest terraces are ~1.7 Ma. Within this sequence, several relationships exist between soil morphology and terrace chronology. On terraces older than ~14,500 yr, argillic horizon development generally increases with terrace age with maximum development occurring in soils of the oldest terraces. $CaCO_3$- and SiO_2-cemented duripans are found in soils on terraces that are late middle Pleistocene and older. By virtue of their physical and chemical properties, duripans are very resistant to erosion, and therefore provide stable records of $CaCO_3$ and SiO_2 accumulation throughout multiple cycles of loess deposition onto the terrace treads, pedogenesis, and partial erosion. Mean duripan thickness increases with age to a maximum of 0.66 m on the oldest terraces. Our results suggest that a geomorphic surface age of approximately 130,000 yr is required to form the initial plugged horizon that is characteristic of a duripan. $CaCO_3$ and SiO_2 accumulation is most rapid in duripans occupying geomorphic surfaces with ages ranging from 130,000 to 300,000 yr. After this, apparent accumulation rates decrease and little additional accumulation of these cementing agents occurs with time.

Introduction

Modern investigations and mapping of the geology of the western Snake River Plain (WSRP), reviewed by Malde (1991) and Othberg (1994), incorporated detailed study of the river terraces, lava flows, soils, and basin structure. These investigations demonstrate the relatively long record of episodic terracing of the Boise Valley, which probably was caused by multiple periods of glacial climate and base-level change during the Pleistocene. Coarse-gravel deposits compose eight terraces that have been mantled by loess of varying thickness. The last major Pleistocene depositional event was the Bonneville Flood, which left slack-water deposits on lower terraces. The terrace ages thus range from approximately 14,500 years ago to early Pleistocene.

Previous soil investigations have provided a wealth of information on soil characteristics in this area. Within the Boise Valley there is a relative uniformity in soil-forming factors, with the exception of the ages of surfaces. Soils of the Boise Valley terraces commonly have illuvial accumulations of silicate clay, SiO_2, and $CaCO_3$ (Collett 1980). One of the more striking features of Boise Valley terrace soils older than late Pleistocene is the presence of *duripans.* A duripan is defined by Soil Taxonomy as "a subsurface horizon that is cemented by silica to the degree that fragments from the air-dry horizon do not slake during prolonged soaking in water or in HCl" (Soil Survey Staff 1975). The duripans are morphologically equivalent to caliche layers that have been described throughout the geological and soil science literature. By definition, duripans are primarily cemented by opaline SiO_2 in contrast to petrocalcic horizons that are primarily cemented by $CaCO_3$ (Soil Survey Staff 1994; Nettleton and Peterson 1983). In semiarid environments a gradation exists between soil horizons where $CaCO_3$ is the dominant cementing agent and those where silica assumes importance as a cementing agent (Blank 1987).

With the current understanding of the terrace chronology, it is now possible to assign ages to specific soil features. The purpose of this study is to relate soil development on Boise Valley terraces to the chronology of the terrace sequence.

Setting

Geology and Geomorphology

The Boise Valley refers to the lower valley and terraces of the Boise River where it crosses the WSRP (Figure 1). The Boise River originates in the Sawtooth and Smokey Mountains of central Idaho where it drains an area of mountainous terrain before it enters WSRP near Lucky Peak Dam southeast of Boise. The Boise Valley extends from the mountain front along the northeastern edge of the WSRP to the confluence of the Boise and Snake Rivers.

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The western Snake River Plain is a graben which probably formed through rifting that started about 17 Ma (Malde 1991). Prolonged subsidence resulted in entrapment of the drainage and filling of the basin with Miocene and Pliocene sedimentary and volcanic rocks. Subsidence continued at least to the middle Pleistocene, but the predominant basin filling of the Pliocene was followed by widespread entrenchment and removal of basin deposits during the Pleistocene (Othberg 1994).

Remnants of high-elevation capping gravels in the WSRP appear to culminate the late Pliocene basin fill in the WSRP. This coarsening of the sediment deposited in the WSRP probably was a response to late Pliocene climate change (Othberg 1994). The ancestral Boise River prograded coarse braided-channel gravels westward across the broad, nearly flat surface of the WSRP about 1.7 Ma (Othberg 1994; Othberg et al. 1995). At this time river flood plains were about 150 m higher than present levels. A changeover from basin filling to incision occurred shortly after these gravels were deposited. Incision initiated the widespread entrenchment and removal of basin deposits and the development of gravel terraces during the Pleistocene (Othberg 1994). The most complete terrace sequence is located near the south side of the city of Boise (Figures 1 and 2).

Othberg et al. (1995) interpreted a geochronology for the terraces based on paleomagnetic polarity, radiometric dates of lavas emplaced on several of the terraces, and correlation to oxygen isotope stages. O'Connor's (1993) study of the Bonneville Flood and the mapping of Bonneville Flood sediment by Othberg and Stanford (1992) have shown that Bonneville slack-water deposits

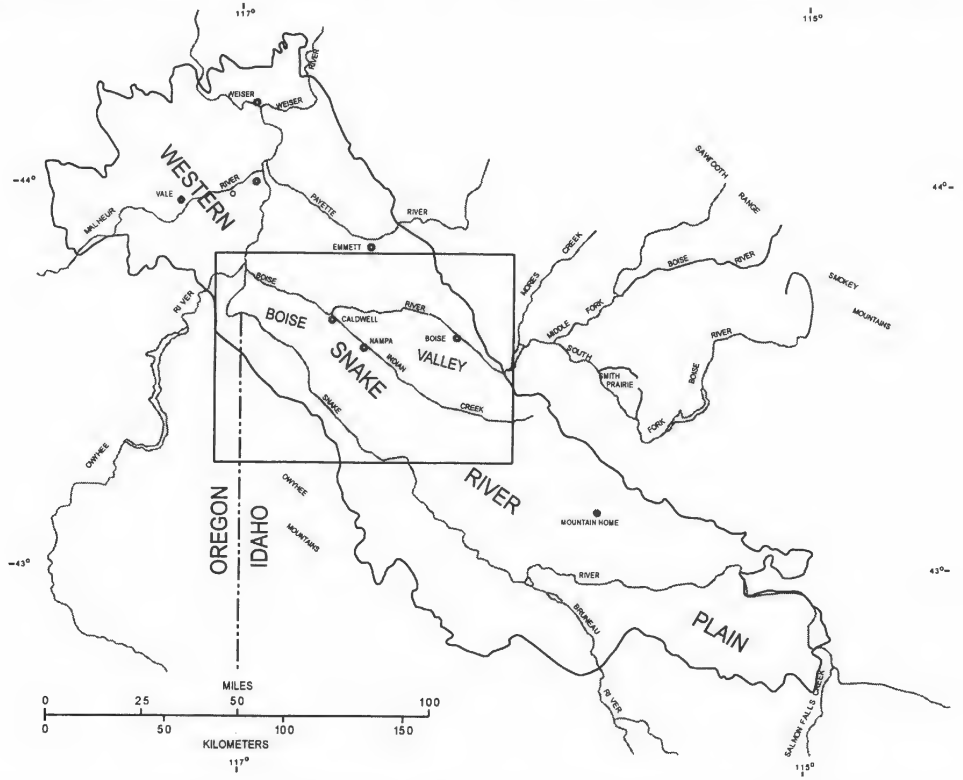

Figure 1. Location of the Boise Valley and the western Snake River Plain. Expanded area of inset (next page) shows the distribution of terraces. Lines A-A' and B-B' represent approximate locations of the east and west diagrammatic profiles in Figure 2. Duripan sample locations are indicated by: W, Whitney terrace; S, Sunrise terrace; G, Gowen terrace; TM, Tenmile terrace.

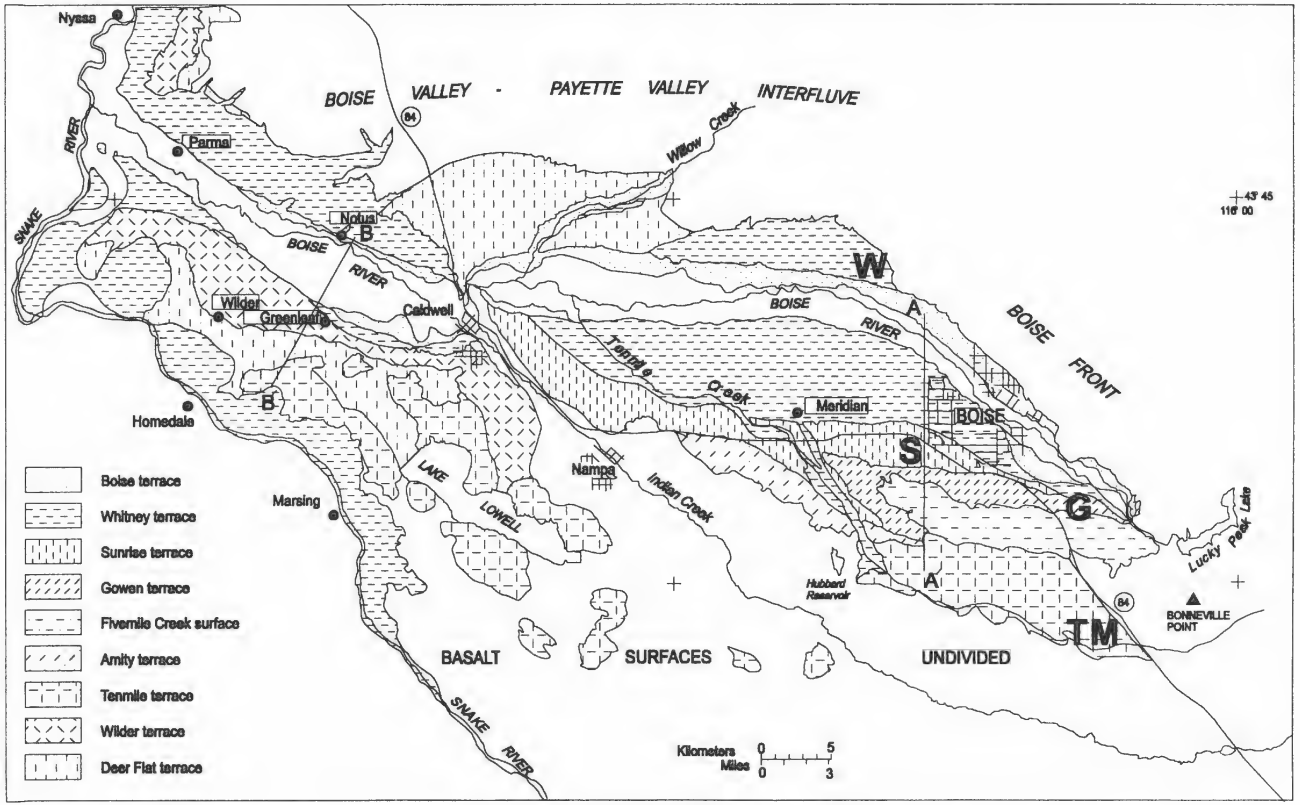

Figure 1. (Continued.)

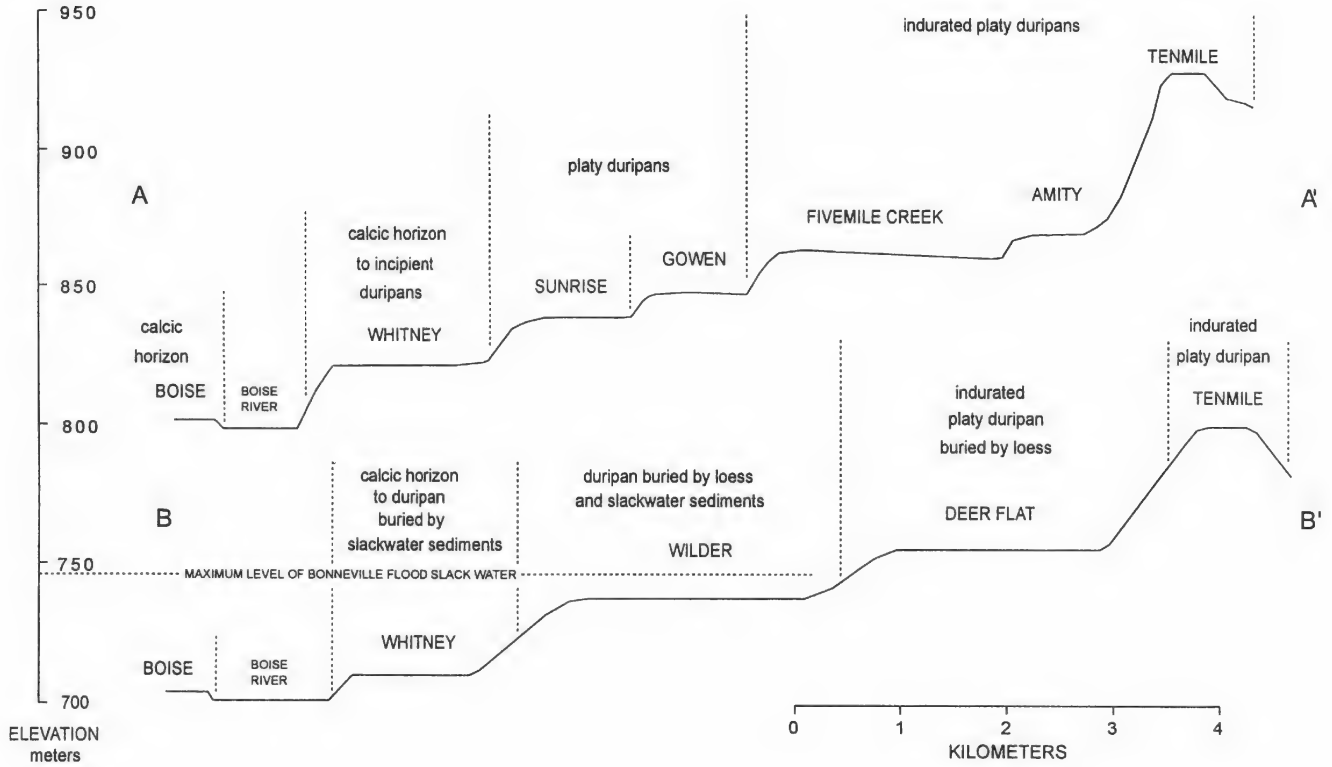

Figure 2. Diagrammatic profiles of the eastern and western Boise Valley terraces and the distribution of soil characteristics on those terraces.

provide a 14,500-yr stratigraphic marker in the Boise Valley and adjacent Snake River valley.

Othberg (1994) presented arguments for correlating the Pleistocene terrace gravels of the Boise Valley with episodes of glacial climate. A detailed study of alluvial-gravel deposition in southeastern Idaho suggests a direct relationship between lowered average annual temperatures and periods of increased gravel deposition on both alluvial fans and mainstream terraces (Pierce and Scott 1982). During periods of colder climate, sustained Peak discharges of the ancestral Boise River may have been at least ten times greater than those observed today (Pierce and Scott 1982. Periodically during the Pleistocene, incision of the western Snake River Plain, including the Boise Valley, appears to have exceeded subsidence in the basin. The sequence of terraces probably formed during many of the episodes of Pleistocene climate change through repeated periods of downcutting followed by coarse gravel deposition. Coupled with dating of basalts on terraces, correlating the sequence to the oxygen isotope stages provides an estimate of the age of each terrace (Figure 3).

Pleistocene Terraces

Each of the gravel terraces of the ancestral Boise River are inset into pre-Quaternary basin-fill sediment. The terrace treads range from 3 m (youngest) to 150 m (oldest) above the present river flood plain. The terrace sequence in the Boise Valley is best preserved south of Boise (Figure 2, profile A-A'). The terrace sequence there, increasing in age and height above the present Boise River, is Boise, Whitney, Sunrise, Gowen, Fivemile Creek (basalt capped), Amity, and Tenmile.

The oldest terrace in the Boise Valley, the Tenmile terrace, is composed of the Tenmile Gravel. Stratigraphically, the Tenmile Gravel is younger than 1.76 Ma (Van Domelen and Rieck 1992; Othberg, 1994). A minimum age for both the Tenmile terrace and the Tenmile Gravel is the $^{40}Ar/^{39}Ar$ date of 1.580 ± 0.085 Ma from basalt capping the first terrace cut into the Tenmile Gravel. Based on correlation with oxygen isotope stages 60 or 62 (Figure 3), the Tenmile terrace is estimated to be approximately 1.7 Ma. All succeeding terrace gravels are younger than the Tenmile Gravel and at least as old as Bonneville Flood sediment dated at 14,500 ^{14}C yr B.P. (Currey 1990). Figure 3 shows the estimated age of each terrace.

Water of the Bonneville Flood was hydraulically ponded upstream of the southern gorges of Hells Canyon. Fine-grained slack-water sediment was deposited by the ponded waters within the western part of the Boise Valley and similar valleys in the WSRP. These thin-bedded silts of the Bonneville Flood mantle the lower three terraces within the western Boise Valley (Figures 1 and 2). The 14,500-year age of the Bonneville Flood provides a minimum date for the terrace sequence and the soil developed on the surface of the Bonneville Flood sediment. Othberg (1994) suggested that the youngest terrace, the Boise terrace, is about the same age as the Bonneville Flood sediment.

Soils

Soil formation can be assessed by using an inductive state-factor approach (Jenny 1980). Site factors (parent material, physiography) and flux factors (climate, organisms) interact over time to produce a given set of chemical, physical, and morphological properties (Buol et al. 1989). Within the western Snake River Plain, there is little variation in site and flux factors affecting soil genesis—climate and vegetation are fairly uniform across the area and presumably have been in the past as a result of the fairly uniform physiography. Modern terrace soils have formed under sagebrush/steppe vegetation with ~28 cm of average annual precipitation and a mean annual temperature of ~10ß C (Collett 1980). Loess is the major soil parent material and has been deposited directly on top of terrace gravels except where basaltic lavas were emplaced. The loess is thinner on older surfaces and thickens in the direction of the Snake River. Because of the relative uniformity of parent material, physiography, climate, and vegetation on terraces of the Boise Valley, most of the differences in soil development appear to be a function of time and, therefore, related to the respective terrace ages. Thus, soils of the Pleistocene terraces represent a chronosequence that can be used to assess the influence of terrace age on pedogenic processes and features.

Bonneville Flood slack-water sediments were deposited on lower terraces near the Snake River, and are present below an elevation of about 740 m and above the late Holocene flood plains. Where

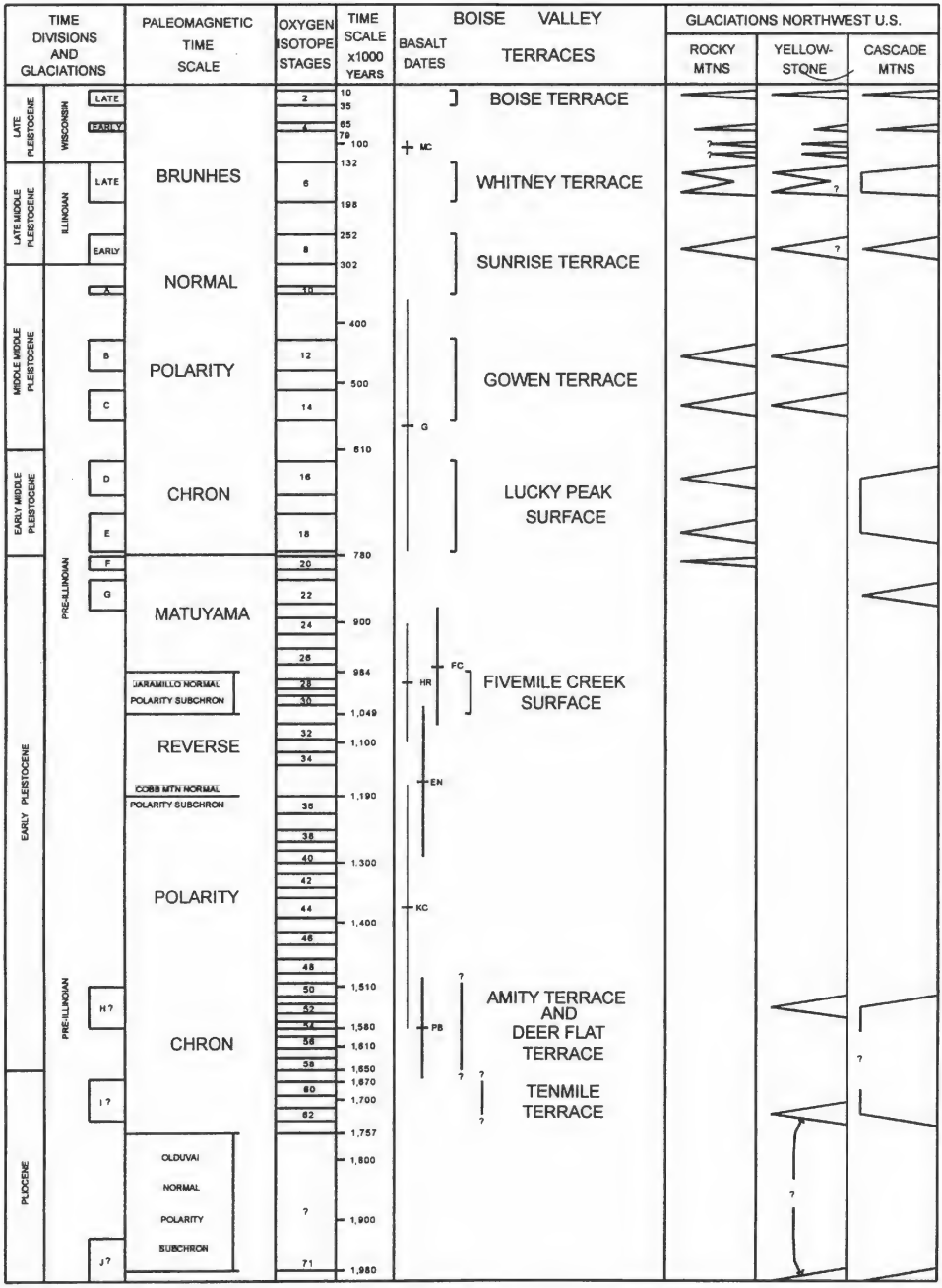

Figure 3. Age and correlation of Boise Valley terraces with glaciations of the northwestern United States and the marine oxygen-isotope cold stages as adapted from Richmond and Fullerton (1986, Chart 1), Ruddiman et al. (1986), Shackleton et al. (1990), and Cande and Kent (1992). Abbreviations for basalt units: MC, Mores Creek; G, Gowen terrace; FC, Fivemile Creek; HR, Hubbard Reservoir; EN, East Nampa; KC, Kuna City; PB, Pickles Butte.

present, these Bonneville Flood sediments have reset the process of soil development through deep burial of existing soils with new sediment. We have observed strongly cemented soil horizons that are overlain with up to 2 m of Bonneville Flood sediments. Minimal pedogenesis has taken place within these sediments and has been limited to some redistribution of $CaCO_3$ and formation of soil structure in the B horizon.

Soils of the Boise Valley terraces are classified as Aridisols according to Soil Taxonomy and often contain argillic horizons and duripans (Collett 1980; Soil Survey Staff 1994). Calcium carbonate is the primary cementing agent in Idaho duripans, but a significant associated chemical component is silica in the form of secondary opal, sepiolite, and palygorskite (Blank and Fosberg 1991).

It is generally recognized that duripan formation requires a source of relatively soluble SiO_2 in addition to the presence of $CaCO_3$ (Soil Survey Staff 1975). In many areas where duripans are extensive, volcanic glass serves as this source (Chadwick et al. 1987; Chadwick et al. 1989). Research in Idaho, however, has suggested that recycling of biogenic opal and emplacement of loess and subsequent weathering may be more important than volcanic glass in providing soluble SiO_2 for duripan formation (Blank 1987; Fosberg et al. 1991).

Materials and Methods

Soil descriptions, particle-size distribution, and chemical properties for soil series representing stages of increasing soil development and age were obtained from existing soil surveys (Priest et al. 1972; Collett 1980), and field reconnaissance. Existing soil profile descriptions were reinterpreted using current horizon designations and descriptions (Soil Survey Staff 1994). In an effort to quantify $CaCO_3$ and SiO_2 accumulation in duripans representing the various-aged terraces, samples were obtained from upland exposures on the Whitney, Sunrise, Gowen, and Tenmile terraces (Figure 1). At each of the four sites, average duripan thickness was determined and 10-20 subsamples were collected across the vertical and lateral exposure of the duripan. These subsamples were composited and ground to pass a 1-mm sieve for subsequent analyses. $CaCO_3$ equivalent was determined using acid neutralization and back titration (U.S. Salinity Laboratory Staff 1954). Opaline Si was determined using Tiron and ammonium oxalate extractions (Kodama and Ross 1991); extracts were analyzed for Si using inductively coupled spectroscopy. All analyses were performed in triplicate.

Soil Characteristics and Pedogenesis

Soil formation on terraces of the Boise Valley appears to have occurred episodically and has undoubtedly been affected by the variations in soil moisture, vegetation, and soil temperature occurring during the Pleistocene. These conditions give rise to complex soil profiles, especially in soils occupying the older geomorphic surfaces (Blank 1987; Fosberg et al. 1991). Sequences of up to three buried soils formed in loess have been observed on some of the lower terraces, indicating that periods of loess deposition were interspersed with episodes of pedogenesis. The fact that this sequence of buried soils is not ubiquitous in the Boise Valley further suggests that periodic, widespread stripping of soil and/or loess from the valley terraces has occurred during the Pleistocene.

Despite the complex cycles of pedogenesis, soils of the Boise Valley terrace system exhibit a range in development that reflects the ages of geomorphic surfaces they occupy. Five soil series described and mapped in the valley approximate the range of soil development observed on the terraces (Othberg and Fosberg 1989; Othberg 1994). Listed in order of increasing soil development, they are the Greenleaf, Power, Purdam, Elijah, and Chilcott Series (Priest et al. 1972; Collett 1980). The youngest of these, the Greenleaf soil, formed in Bonneville Flood slack-water sediments. The four older soils—Power, Purdam, Elijah, and Chilcott—have loess as a common parent material and best represent a developmental sequence of late-middle to early Pleistocene soils in the Boise Valley. This soil sequence illustrates several changes in soil morphological properties that are time-dependent, including accumulation of layer silicate clays, $CaCO_3$, and opaline SiO_2. Accumulation of these soil constituents generally increases with soil age, and as a result, reflects the relative ages of the geomorphic surfaces they occupy.

Clay Accumulation

The four soils that represent late middle to early Pleistocene terraces of the Boise Valley contain subsurface zones of clay accumulation referred to as argillic horizons (Soil Survey Staff 1994). Argillic horizon development can be used as a relative indicator of soil age within a given geographic setting (Soil Survey Staff 1975; Birkeland 1984 1985). The presence of an argillic horizon implies sufficient landscape stability to allow layer silicate clay formation from weathering of primary minerals, as well as translocation of clays within a soil profile. It is generally recognized that substantial clay accumulation within a soil must be preceded by leaching of $CaCO_3$ (Duchaufour 1982). The presence of $CaCO_3$ maintains colloidal particles in an aggregated or flocculated state; upon removal of $CaCO_3$, clay colloids become dispersed and can then be more easily transported by water percolating downward through the soil.

In general, clay accumulation increases in soils of geomorphic surfaces of increasing age. Soils of the Whitney terrace such as Power have relatively weakly developed silt loam- to silty clay loam-textured, argillic horizons (Collett 1980). On the other end of the developmental/age sequence, Chilcott soils of the Tenmile surface exhibit strongly developed argillic horizons with an abrupt textural change (relative to the overlying horizon) and silty clay textures (Collett 1980; Soil Survey Staff 1994); clay contents in the argillic horizon of Chilcott soils are as high as 49% (Sandoval et al. 1959). Soils of the Sunrise and Gowen surfaces generally exhibit argillic horizon development that is intermediate to that of Power and Chilcott soils; Stuart et al. (1961) reported a clay content of 21% in the Bt (argillic) horizon of a Purdam soil on the Sunrise terrace.

Clay accumulation as a means of assessing pedogenesis in soils of the Boise Valley must be used cautiously. Field evidence suggests that multiple cycles of loess deposition, soil formation, and erosion have occurred throughout the Pleistocene. Older soils of the region show evidence of differential stripping to the duripan followed by loess deposition subsequent argillic horizon development that postdates the duripan (Blank 1987; Fosberg et al. 1991). Loess/paleosol sequences can be observed in some terrace exposures in the Boise Valley, providing evidence of these cycles. However, these sequences are not uniformly present throughout the terrace system, again suggesting that extensive denudation of the landscape has occurred. As a result, the A and Bt horizons of modern soils may be considerably younger than the geomorphic surface that they occupy. Also, soils exhibiting different stages of argillic horizon development sometimes occur together and may be mapped as complexes on the terraces of the Boise Valley (Collett 1980). The genesis of these complexes is not well understood, but we suspect it may also be related to differential erosion of the landscape and subsequent cycles of loess deposition and pedogenesis. It therefore may be difficult to determine which developmental stage is 'typical' for a given geomorphic surface. Finally, urban development in the area has drastically altered the modern soils, making it difficult to find exposures that contain a complete soil-stratigraphic record.

Duripan Development and Accumulation of $CaCO_3$ and SiO_2

Duripans provide an excellent means of assessing pedogenesis because of their inherent physical and chemical properties. After some initial stage of development has been attained, duripans become extremely resistant to subsequent weathering and erosion. This may be extremely important in an area like the Boise Valley where cycles of erosion have apparently removed other, less-stable products of pedogenesis such as argillic horizons. Under these conditions, it seems reasonable to expect that duripan development will be more closely related to the age of a geomorphic surface than will pedogenic development of the overlying soils.

Duripan morphology appears to change systematically with terrace age in the Boise Valley. Our results suggest that a geomorphic surface age of ~130,000 yr (Whitney terrace, Figure 3) is required in the Boise Valley to form the initial plugged horizon that is characteristic of a duripan. Duripans of the 130,000-yr Whitney terrace are relatively thin (Figure 4a), weakly cemented, and are often laterally discontinuous when observed across large exposures. These duripans have a cemented matrix and appear to represent stage III silica accumulation (Harden et al. 1991). Similar Si accumulation stages have been reported in soils of geomorphic surfaces in Nevada with a minimum

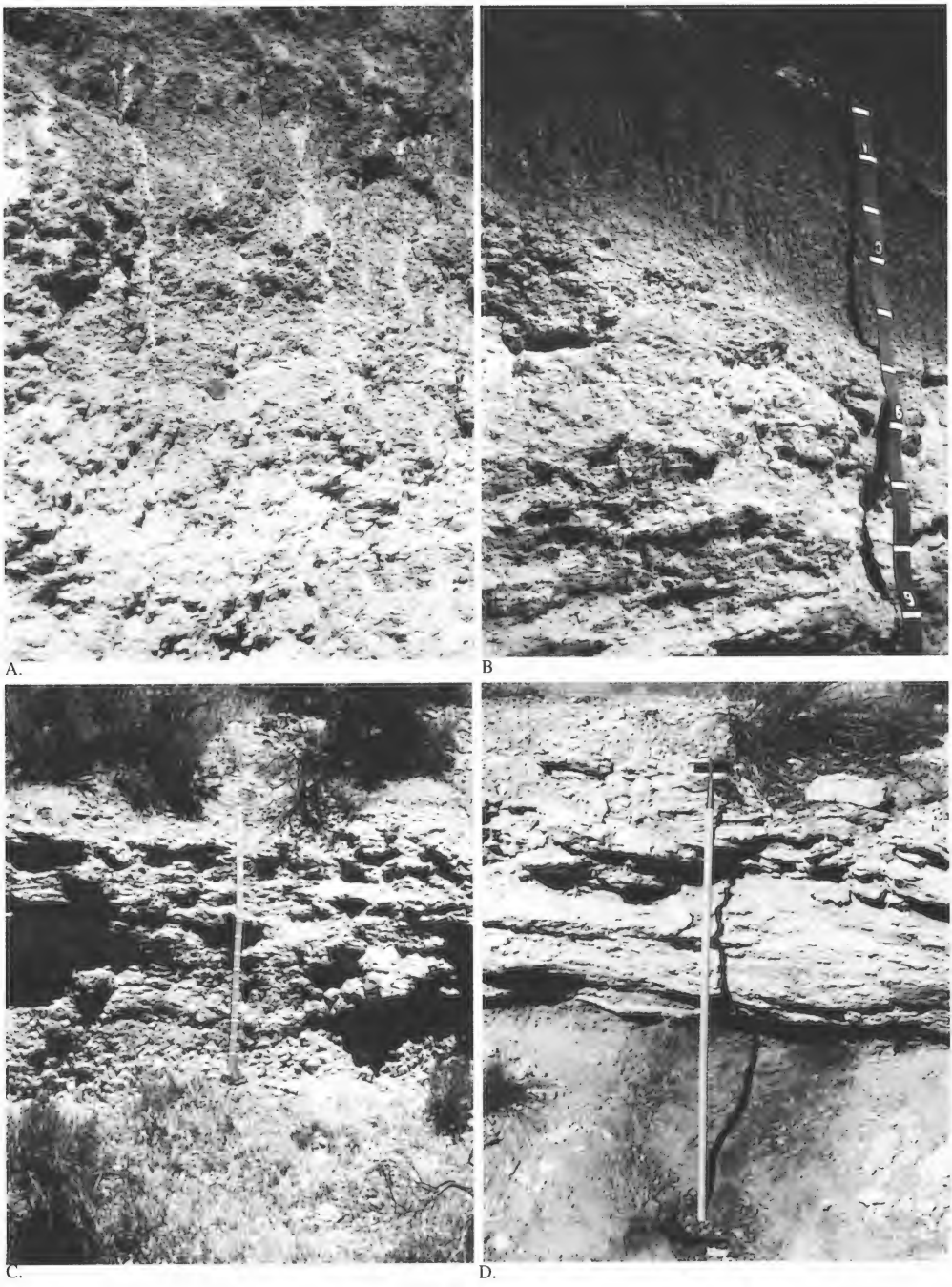

Figure 4. Soil profiles showing duripans for: (a) Whitney terrace (US nickel in center of exposure for scale); (b) Sunrise terrace (scale in decimeters); (c) Gowen terrace (scale tape is ~1.5 m long); (d) Tenmile terrace (tool for scale is ~1.2 m long).

age of 145,000-190,000 yr (Harden et al. 1991). In contrast, duripans of the Tenmile terrace (1.7 Ma) are the thickest of those observed in the Boise Valley and have strongly cemented, laminar plates that average up to 5 cm in thickness (Figure 4d). This accumulation stage IV has been reported in Nevada in soils occupying geomorphic surfaces with minimum ages of 270,000-440,000 yr (Harden et al. 1991). Intermediate development is seen in duripans on the Sunrise and Gowen terraces (Figure 4b and Figure 4c).

Accumulation of $CaCO_3$ in soils has been extensively used by geologists and soil scientists as a relative dating tool in arid and semiarid landscapes of the western US (Gile and Grossman 1979; Machette 1985; Harden 1982; Reheis et al. 1989). To a lesser degree, SiO_2 accumulation has also been quantified as an indicator of pedogenesis and geomorphic surface age. We examined both $CaCO_3$ and SiO_2 content of duripans from the Whitney, Sunrise, Gowen, and Tenmile surfaces and used these data to compute an accumulation index for each site. The accumulation index was obtained by multiplying $CaCO_3$ or SiO_2 concentrations by a relative duripan thickness factor. Because the Tenmile duripan had the greatest average thickness (0.66 m), it was assigned a factor of 1.0; factors for the other duripans were calculated by comparing their average thickness to that of the Tenmile duripan. These factors were 0.98 for the Gowen duripan, 0.80 for the Sunrise duripan, and 0.45 for the Whitney duripan. The $CaCO_3$ accumulation index reflects the average $CaCO_3$ equivalent of each duripan multiplied by a relative thickness factor. For example, the thickest duripan (Tenmile surface) is assigned a depth factor of 1.0; other duripans are assigned a factor based on their thickness relative to that of the Tenmile duripan. Figure 5a indicates that $CaCO_3$ accumulation rates are greatest in duripans of the middle-Pleistocene-aged surfaces (Whitney, Sunrise, and Gowen terraces). Little additional accumulation is seen in the duripans of the early-Pleistocene Tenmile terrace. Opaline SiO_2 accumulation indexes are shown in Figure 5b, and comparison with Figure 5a indicates that accumulation rates of SiO_2 mirror those of $CaCO_3$. The maximum accumulation rates for both $CaCO_3$ and SiO_2 appear to occur in duripans of terraces with ages less than ~300,000 yr. Both curves support data presented by Harden et al. (1991) that indicate a decrease in accumulation rates with increasing time. The decrease in accumulation rates has been attributed to mineral weathering kinetics, decreases in dust accumulation, and/or greater erosion of older soils (Harden et al. 1991). While any of these explanations seem plausible for the Boise Valley terrace system, it also seems likely that the decrease in $CaCO_3$ and SiO_2 accumulation rates in duripans may result from the change in soil hydraulic properties that accompanies cementation of the soil matrix. As proposed by Gile et al. (1966), once a horizon becomes plugged through cementation of the soil matrix, downward percolation

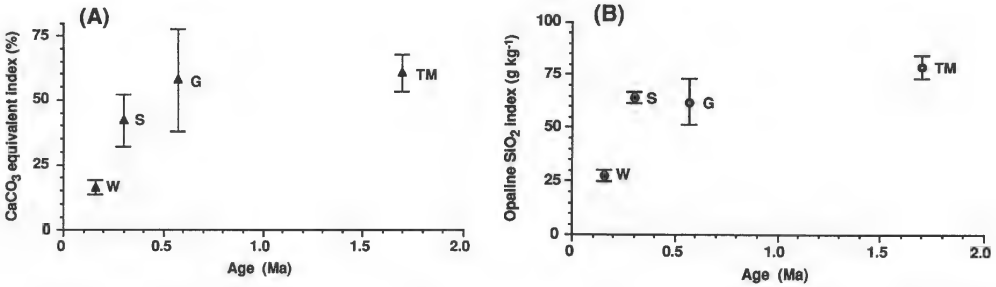

Figure 5. (a) $CaCO_3$ equivalent index for duripans in the Boise Valley formed on different-aged geomorphic surfaces. Index is calculated by multiplying average $CaCO_3$ equivalent by a relative duripan thickness factor. (b) Opaline SiO_2 index for duripans in the Boise Valley formed on different-aged geomorphic surfaces. Index is calculated by multiplying average opaline SiO_2 content by a relative duripan thickness factor. Vertical bars represent one standard deviation about the mean of replicate samples. Abbreviations: W, Whitney terrace; S, Sunrise terrace; G, Gowen terrace; TM, Tenmile terrace.

of soil solution is severely restricted and lateral movement may occur. As a result, continued formation of the duripan is by vertical accretion, a process that affects less of the soil volume than the initial plugging of the soil matrix.

Although initial silicification may be very rapid in soils containing volcanic glass (Chadwick et al. 1989), data from the Boise Valley indicate that duripan formation in terraces requires a minimum of ~130,000 yr. These soils do not contain significant quantities of volcanic glass, and, as proposed by Flach et al. (1969), may therefore may require the prolonged, slow weathering of feldspars and ferromagnesian minerals to produce and accumulate sufficient SiO_2 cement to form a duripan. Once formed, these duripans appear to be able to persist through erosional cycles and provide a pedogenic record of silica and carbonate accumulation.

Conclusions

A sequence of Pleistocene terraces in the Boise Valley provides a chronology of geomorphic surfaces from approximately 14,500 yr to 1.7 Ma. Soils of this sequence exhibit a range in development that is related to terrace age. In soils with loess parent material, subsurface clay accumulation generally increases with terrace age as does thickness of duripans and accumulation of $CaCO_3$ and SiO_2. In the Boise Valley $CaCO_3$- and SiO_2-cemented duripans occur on the terraces that are late middle Pleistocene and older. An estimated age of approximately 130,000 yr is required to form the initial plugged horizon that is characteristic of a duripan. Although features such as clay accumulation may be lost in cycles of erosion, the relatively resistant duripans provide a stable, long-term record of soil development.

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Patterns of Atmospheric Nitrogen Dioxide in Kelowna, British Columbia

Abstract

Prior to 1994, atmospheric monitoring in the central Okanagan Valley region of British Columbia (BC) was restricted to ozone analysis and sporadic determinations of total suspended particulates, and dust. In May 1994, a BC Government air monitoring station measuring PM_{10}, CO, NO_x, O_3 and SO_2 was installed in the city of Kelowna. To complement the data obtained at this fixed location this study measured the spatial distribution of nitrogen dioxide gas at various locations throughout Kelowna. Twelve sites were chosen for a twelve month monitoring program (June 1994 to May 1995). Sampling, over 7 to 10 day periods, was carried out using Palmes passive diffusion tubes; analysis of the trapped NO_2 was determined spectrophotometrically. Estimates of mean accuracy (-4 %), and precision (standard deviation ± 8%), were determined by comparing diffusion tube data with that obtained by the monitoring station. Average daily NO_2 concentrations varied from 8 to 79 $\mu g/m^3$. High concentrations of NO_2 were measured in late July 1994 coincident with a nearby large forest fire. The highest overall values were obtained adjacent to Highway 97, the main traffic route, during a period of stagnant air conditions in late November and early December 1994. Average annual mean values ranged from 21 $\mu g/m^3$ to 50 $\mu g/m^3$, well within the Canadian and US (NAAQS) air quality objectives. The data obtained in this study provides a suitable base from which future comparisons of NO_2 levels, and air quality trends, may be assessed.

Introduction

The largest regional population in the interior of British Columbia (BC) is found in the Okanagan Valley of south central BC. The main city of the region, Kelowna (Figure 1), has experienced a particularly rapid population growth over the past 20-30 years, increasing from about 20,000 in 1970 to in excess of 95,000 today (de Scally and Turchak 1996). There is concern that the air quality in the region is deteriorating due to this population increase. For this reason, the BC Provincial Ministry of Environment, Lands and Parks in 1994 installed a comprehensive atmospheric monitoring station at the KLO Road campus of Okanagan University College (OUC) in Kelowna. This station continuously monitors atmospheric concentrations of inhalable particulate matter (PM_{10}), ozone (O_3), nitrogen oxides (NO_x), carbon monoxide (CO) and sulfur dioxide (SO_2), producing hourly average concentrations of these target pollutants (Josefowich and Reid 1995). Prior to the opening of this station, air quality monitoring for O_3 and total suspended particulates had been carried out on a less regular basis (Richardson and Jensen 1991).

Two aspects of air quality of immediate concern in Kelowna and the Okanagan Valley are: (i) high concentrations of PM_{10}, which may lead to respiratory impairment (Vedal 1993; Vedal 1995), and (ii) the potential for summertime production of high concentrations of ground level O_3 (Reid 1995).

As well as being a strong oxidant, ground level O_3 combined with NO_x, atmospheric hydrocarbons (from automobiles or trees/plants), intense sunlight, high temperatures and static air can lead to the formation of photochemical smog. This smog may be deleterious to health (particularly of the young and elderly), can adversely affect crop production, can attack materials (plastic and rubber) and is unsightly (a yellow/brown haze). Thus the onset of photochemical smog episodes could have serious repercussions to the public health and economy of the Kelowna area. Tourism and agriculture are major industries of this region.

Tropospheric O_3 is produced by a series of reactions which start with nitric oxide, NO (Jeffries 1995; Finlayson-Pitts and Pitts 1997). Natural sources of NO include microbial activity in soils and the interaction of lightning with atmospheric nitrogen and oxygen. However, the major source of NO is high temperature fossil fuel combustion as generated by the transportation sector, Equation (1). NO, in the presence of O_3, is readily oxidized to NO_2, Equation (2). NO_2 is decomposed by UV-A sunlight, Equation (3), releasing an oxygen atom capable of combining with O_2 to produce O_3, Equation (4). As indicated by Finlayson-Pitts and Pitts (1997), these latter two

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Figure 1. Location of the city of Kelowna, Okanagan Valley, British Columbia, Canada.

reactions are the only known methods of tropospheric O_3 production.

$$N_2 + O_2 \xrightarrow{flame} 2\,NO \qquad (1)$$

$$NO + O_3 \longrightarrow NO_2 + O_2 \qquad (2)$$

$$NO_2 \xrightarrow{h\nu\,(\lambda \leq 430\,nm)} NO + O \qquad (3)$$

$$O + O_2 \longrightarrow O_3 \qquad (4)$$

From these equations, it appears that there is no net gain of O_3; one molecule of O_3 is used up and one is produced, resulting in a null cycle. However, O_3 can react photochemically and, in the presence of water, produces the hydroxyl radical, $^{\bullet}OH$.

$$O_3 \xrightarrow{\lambda < 320\,nm} O_2 + O \;;\; O + H_2O \longrightarrow 2\,{}^{\bullet}OH$$

In an atmosphere containing volatile organic compounds (VOC), such as hydrocarbons (RH) the very reactive $^{\bullet}OH$ species can abstract a proton. Further reaction with O_2 gives a peroxy radical, $ROO^{\bullet}$ (Bunce 1994).

$$RH + {}^{\bullet}OH \rightarrow R^{\bullet} + H_2O \;;\; R^{\bullet} + O_2 \rightarrow ROO^{\bullet}$$

These peroxy radicals are also capable of oxidizing NO to NO_2, Equation (5).

$$NO + ROO^{\bullet} \longrightarrow NO_2 + RO^{\bullet} \qquad (5)$$

As a single hydrocarbon molecule is capable of producing several peroxy radicals (Baird 1995), enhanced production of NO_2 by reactions equivalent to Equation (5) can occur. This NO_2 can further react to produce more O_3, via Equations (3)

and (4). So, under appropriate climatic conditions, rather than having a null cycle, a build up of O_3 is obtained in an atmosphere polluted with NO_x and VOC. For example, the complete atmospheric oxidation of methane is represented by:

$$CH_4 + 11\,O_2 \xrightarrow{sunlight,\ NO} CO_2 + 2\,H_2O + 6\,O_3$$

This is an oversimplification because there may also be other products.

Peroxy radicals are not the only species produced by the photochemical oxidation of hydrocarbons. In an atmosphere containing high concentrations of NO and RH, irradiation with sunlight may, through a series of complex photochemical reactions, produce photochemical smog, as indicated by the general equation:

$$RH + O_2 \xrightarrow{sunlight,\ NO} \text{aerosol particles, } O_3,\ NO_x,\ \text{organic nitrates, aldehydes, etc.}$$

To estimate a region's potential for smog generation, data are required on spatial and temporal distributions of NO_x, O_3 and RH, as well as meteorological parameters such as sunlight intensity, temperature and wind motion. Obtaining information on spatial and temporal distributions of NO_x, O_3 and RH requires several monitors to be placed at locations within the sampling region. The high cost of monitoring instruments generally prohibits this approach.

As well as being a fundamental chemical involved in O_3 and photochemical smog production, NO_2 is also recognized as a toxic pollutant, acting as a respiratory irritant and plant growth suppressant (Hilborn and Still 1990). The spatial distribution of NO_2 can readily be measured using inexpensive passive diffusion tubes (Palmes 1976, Campbell 1988, Shooter 1993, Campbell et al. 1994), consequently this gas has been selected as the target analyte for this study. NO_2 was measured at various locations within the city of Kelowna throughout a twelve month sampling period.

Methods

Passive diffusion tubes, as described by Shooter (1993), are 7 cm x 1 cm acrylic cylinders with one end open to the atmosphere. The closed end houses a stainless steel mesh impregnated with an aqueous solution of triethanolamine. The tubes are mounted on poles, walls, trees etc. using a specially designed bracket. Atmospheric NO_2 enters the diffusion tubes by molecular diffusion and reacts with the triethanolamine. The amount of reaction is proportional to the concentration of NO_2 in the air. After an appropriate sampling period (7 to 10 days), the tubes are returned to the laboratory where the triethanolamine in the tubes is treated with solutions of sulfanilamide and N-1-naphthylethylenediamine dihydrochloride, producing a purple solution of an azo dye. The intensity of the purple color, as determined spectrophotometrically (λ = 540 nm), is directly proportional to the amount of NO_2 that has interacted with the triethanolamine. The experimental results are converted to a daily mean concentration in units of ppbv, parts per billion (1 part in 10^9) NO_2 by volume. The units are finally converted to $\mu g/m^3$, i.e. μg of NO_2 per m^3 air.

Method development and testing, and sample site selection took place in May 1994. Diffusion tubes were initially placed at 26 locations throughout Kelowna. Sites were chosen that were representative of various areas of the city (e.g. light industrial, commercial, residential, semi-rural) with a greater emphasis placed on major traffic areas. Sampling and analyses were carried out during June, July and August, 1994 as part of a Deep River Science Academy Research Project (a summer camp for gifted high school students). On the basis of the data collected, 12 of the sites were further monitored from September 1994 to June 1995. These sites included those found in the preliminary measurements to have the highest NO_2 concentrations. The residential and semi-rural sites, all of which indicated low NO_2 concentrations, were excluded because the site at the KLO Road monitoring station, which was retained, appeared to be representative of these locations.

A map of Kelowna (Figure 2) indicates the location of the 12 sampling sites. Main features included are Okanagan Lake and the major traffic routes, Highways 97 and 33. Kelowna, at an elevation of 350 m is situated near the middle of a 100 km long narrow north-south valley having mountains of approximately 1,500 m immediately to the east and west.

To estimate the accuracy of the technique, diffusion tubes were mounted at the KLO Road Provincial monitoring site (Site-1) and the analyses compared to the BC Provincial monitor data. To improve the precision of the method sampling tubes were always mounted as pairs. Tests were made of laboratory blanks and field blanks.

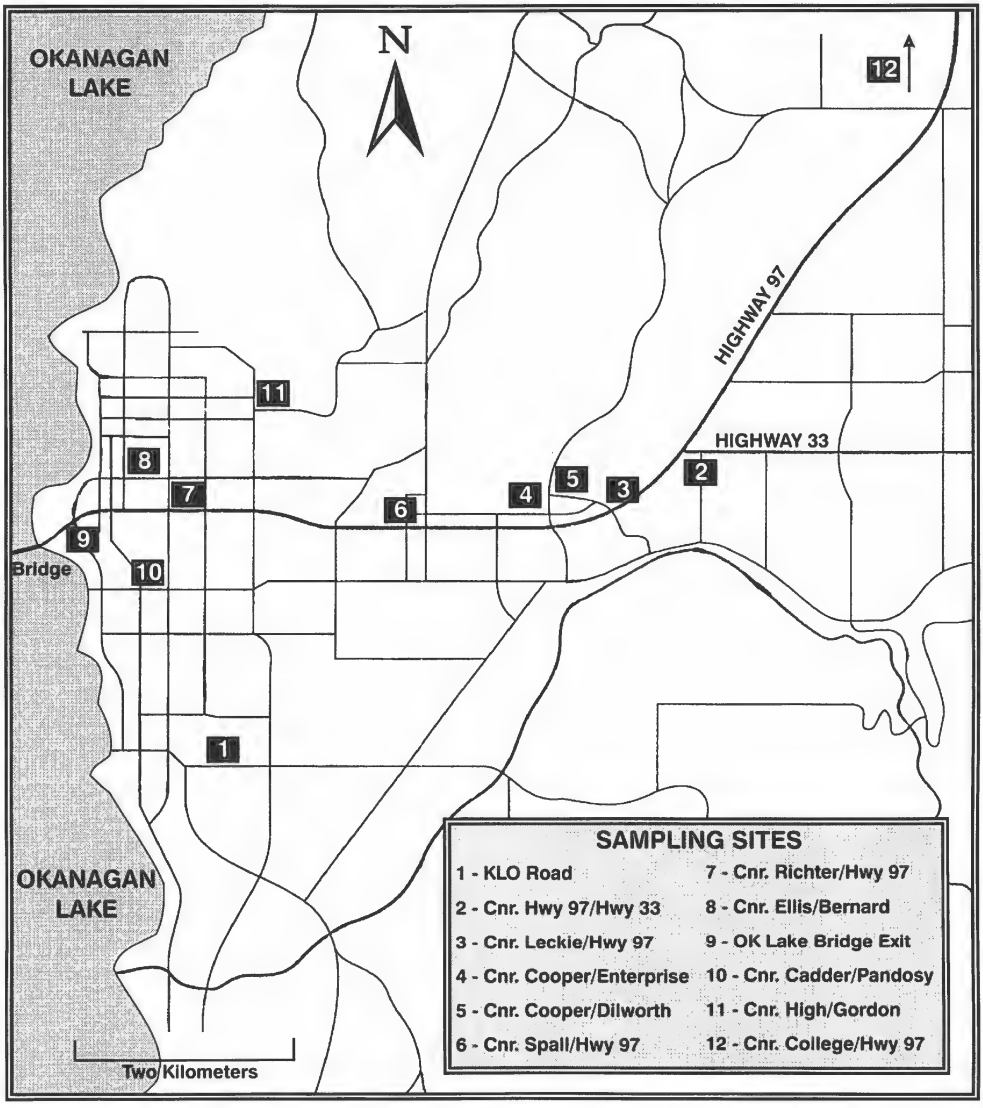

Figure 2. Location of NO_2 sampling sites within the city of Kelowna.

Data Evaluation

As part of a quality assurance and quality control program, the BC Provincial NO_2 monitor at KLO Road is calibrated and checked on a daily basis (Josefowich and Reid 1995). Differences between the Site-1 diffusion tube values and those generated by the monitor were interpreted as being solely due to the inherent inaccuracy of the diffusion tube method. Comparative data are presented in Figure 3 for 48 sampling periods between June 9, 1994 to June 8, 1995.

For the 48 samples, the mean value obtained by the BC Provincial monitor was 12.0 $\mu g/m^3$ (SD 3.8 $\mu g/m^3$) and the diffusion tubes value was 11.6 $\mu g/m^3$ (SD 4.0 $\mu g/m^3$). On average the diffusion tube values were 4% lower. The 90

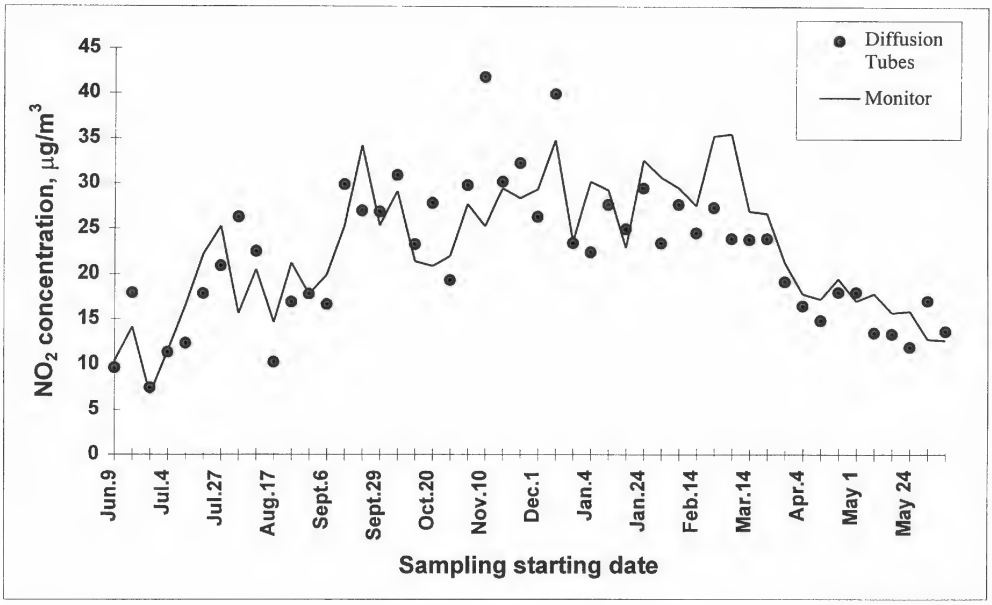

Figure 3. A comparison of the daily average NO_2 concentrations measured at the KLO Rd. sampling site by the BC Provincial Monitor and by the diffusion tube method (this study).

interpercentile range of differences between individual diffusion tube measurements and those generated by the monitor was -25% to + 26%. On comparing the values obtained from 46 duplicate pairs of tubes the relative standard deviation was 8.1%. These values compare favorably with passive diffusion tube measurements obtained by Shooter (1993) who quotes an agreement of 15% with other measurement techniques and a precision of 10%, which are of similar magnitude to those reported in other studies (Campbell 1988; Gair et al. 1991; Shooter et al. 1993; Ashenden 1994).

If field blank corrections are included the mean difference decreases from -4% to -15%. Because of this large negative bias, presumably due to leakage and/or contamination, field blank corrections were neglected in subsequent calculations.

Results and Discussion

Table 1 lists the NO_2 concentrations for the 12 sites monitored from June 1994 to June 1995. Gaps in the data are through loss of diffusion tubes, due to their being insecurely attached, or through vandalism (only a minor problem).

From this data set, interpretations are made using (i) the annual arithmetic mean values (AAM), and (ii) the highest sample period values. The AAM values are listed at the foot of Table 1; the highlighted (boxed) values in Table 1 indicate the 3 highest sample period values determined at each site.

The highest AAM values obtained in this study were 49 and 50 $\mu g/m^3$ measured at Sites 7 and 6, respectively. Both of these sites are on Highway 97, at two of the city's busiest intersections. These values are lower than the AAM listed as the "Maximum Desirable" Canadian Air Quality Objective for NO_2 of 30 ppbv (about 60 $\mu g/m^3$) (Hilborn and Still 1990). They are also substantially lower than the US National Ambient Air Quality Standard (NAAQS) for an AAM listed as 100 $\mu g/m^3$ (Nadakavukaren 1995). For comparison, typical AAM NO_2 values are 9 to 15 $\mu g/m^3$ for rural areas, 28 $\mu g/m^3$ for urban areas (Hewitt 1991) and 85 to 95 $\mu g/m^3$ for metropolitan regions, London (Duncan et al. 1987), New York (Goldstein et al. 1988) and Seoul (Nuki 1996).

Relatively high AAM values, from 38 to 46 $\mu g/m^3$, were also obtained at other sites on Highway 97 (Sites 2 and 3) as well as sites situated

TABLE 1. Daily average NO_2 concentrations ($\mu g/m^3$) measured at 12 sampling sites (see Figure 2) Kelowna, BC, from June 1994 to June1995. The highest 3 values at each site are in bold outline. The final row lists the Average Annual Mean value.

Start	Site	Site	Site	Site	Site	Site	Site	Site	Site	Site	Site	Site
Date	1	2	3	4	5	6	7	8	9	10	11	12
Jun.9	9											
Jun.14	9		32	32	21							
Jun.22	17		41	45	28	62	25	38	51	60	43	
Jun.29	8	21	25	23	13	62	25	38	51	60	43	21
Jul.6	8	21	26	26	15	30	9	25	28	38	23	15
Jul.13	8	23	34	36	19	40	13	32	43	43	32	23
Jul.20	13	34	40	43	21	43	19	40	47	49	41	28
Jul.27	17	47	64	64	41	62	30	55	70	66	55	51
Aug.4	26	49	47	49	26	45	17	43	57	51	38	36
Aug.9	26	43	43	40	30	49	19	47	51	64	32	30
Aug.17	9	32	37	34	20	41	52	36	44	50	36	30
Aug.25	17	38	44	37	23	47	55	40	45	55	38	30
Sept1	18	39	47	44	26	58	66	48	45	61	44	33
Sept.7	17	39	44	43	25		54	41	36	50		33
Sept.15	17	43	46	48		57	54	41	36	50		39
Sept.23	27		59	53	39	57	68	53	60		56	39
Sept.30	27	33	44	37	27	52	0	40	39		35	39
Oct.7	31	43	48	42	28	50	59	45	42		39	29
Oct.14	23	35	40	36	23	41	51	36	35	31	33	32
Oct.22	28	42	52	43	29	51	54	36	44	35	39	28
Oct.29	19	37	40	44	27	49	46	33	32	32	33	32
Nov.5	30	50	60	57	32	60	65	46	47	37	43	35
Nov.11	42	60	63	62	40	69	72	53	52	55	52	39
Nov.18	30	43	54	39	30	43	46	53	62	39	43	32
Nov.24	32	54	65	57	37	65	73	55	46	49	48	48
Dec.3	26	45	48	44	29	50	60	38	36	36	39	32
Dec.13	40	59	68	58	43	79	74	55	49	55	52	45
Dec.20	23	51	62	53	34	58	67	48	43	47	41	31
Dec.29	23	31	45	35	18	40	48	43	42	34	25	20
Jan.5	22	28	43	34	25	38	54	43	33	35	31	25
Jan.11	28	37	40	40	31	47	49	38	31	37	35	29
Jan.18	25	38	52	43	26	50	61	43	42	39	35	31
Jan.25	29	44	53	48	34	47	63	42	35	45	41	34
Feb.1	23	39	38	29	27	45	45	37	31	40	46	28
Feb.8	28	38	41	33	20	38	45	38	40	38	29	24
Feb.15	25	55	56	53	33	61	64	48	42	50	44	32
Feb.21	27	54	51	44	29	50	58	44	43	47	37	29
Mar.1	24	39	38	36	18	39	45	44	51	46	31	29
Mar.8	24	55	57	51	45	60	55	52	54	55	51	38
Mar.15	24	42	52	47	35	57	55	48	43	47	44	33
Mar.22	24	46	49	43	30	51	56	47	52	50	44	33
Mar.29	20	41	42	45	29	52	65	48	42	54	46	26
Apr.5	16	41	40	37	25	51	57	42	43	51	42	26
Apr.12	15	31	36	36	20	43	45	39	40	41	34	22
Apr.20	18	39	39	39	23	49	44	39	51	50	37	23
May1	18	34	33	35	24	49	44	39	51	50	37	22
May 9	13	31	40	37	23	44	48	39	43	49	39	25
May 17	13	41	45	30	24	48	48	37	44	53	36	25
Jun.2	17	39	46	50	31	60	63	46	54	62	46	36
Jun.8	14	36	44	41	25	60	63	46	54	62	46	29
Average	21	38	46	42	27	50	49	43	45	45	38	31

close to the main commercial and industrial areas (Sites 8, 9, 10 and 11). At Site-12, also on Highway 97, but in a semi-rural area outside of the traffic congestion corridor a lower value, 31 $\mu g/m^3$, was obtained. The lowest AAM value, 21 $\mu g/m^3$, was measured at Site-1, adjacent to the KLO Road monitoring station. This is about 40% of the maximum AAM as recorded at Site-6.

At some distance from Highway 97, a decrease in NO_2 concentration is expected, due to less traffic and bulk air motion. This was supported experimentally. Site-3, on Highway 97, had an AAM value of 46 $\mu g/m^3$; Site-4, one block north of Highway 97, a value of 42 $\mu g/m^3$; and Site-5, two blocks north of Highway 97, a value of 27 $\mu g/m^3$.

Maximum sample period values (Table 1) were in the range of 42 to 79 $\mu g/m^3$, falling well within the guidelines of the BC Air Quality "Maximum Desirable" criterion of 200 $\mu g/m^3$ for a 24 hour average (Josefowich and Reid 1995). It should be noted that the values quoted in this paper are averaged over the 7 to 10 days required for sampling and are not "true" 24 hour average values.

The highest sample period values were obtained during two time periods, July 27 to August 4, 1994 and November 11 to December 20, 1994. The first period coincided with a large forest fire south of Kelowna which produced a pall of smoke haze for several days. The thick smoke, having reduced the ground level solar intensity, may have interfered with the photochemical breakdown of NO_2, Equation (3). The second period coincided with an abrupt onset of cold winter temperatures (mean temperatures: October 8.0 °C, November -0.5 °C) (Environment Canada, monthly meteorological reports 1994) coupled with a period of fairly stagnant air (mean wind speed: November 3.1 km/hr) (Environment Canada, monthly meteorological reports 1994). The lower temperatures would slow down the rate of many of the chemical reactions involved in NO_2 consumption; the static air would trap the NO_2 within the narrow confines of the Okanagan Valley.

The seasonal variation of NO_2 concentrations as measured at two representative sampling sites, Site-1 and Site-6, is compared in Figure 4. Maximum values appear in November and December and minimum values from May through August. On average, winter values are slightly higher than those obtained in the summer. In the summer, although

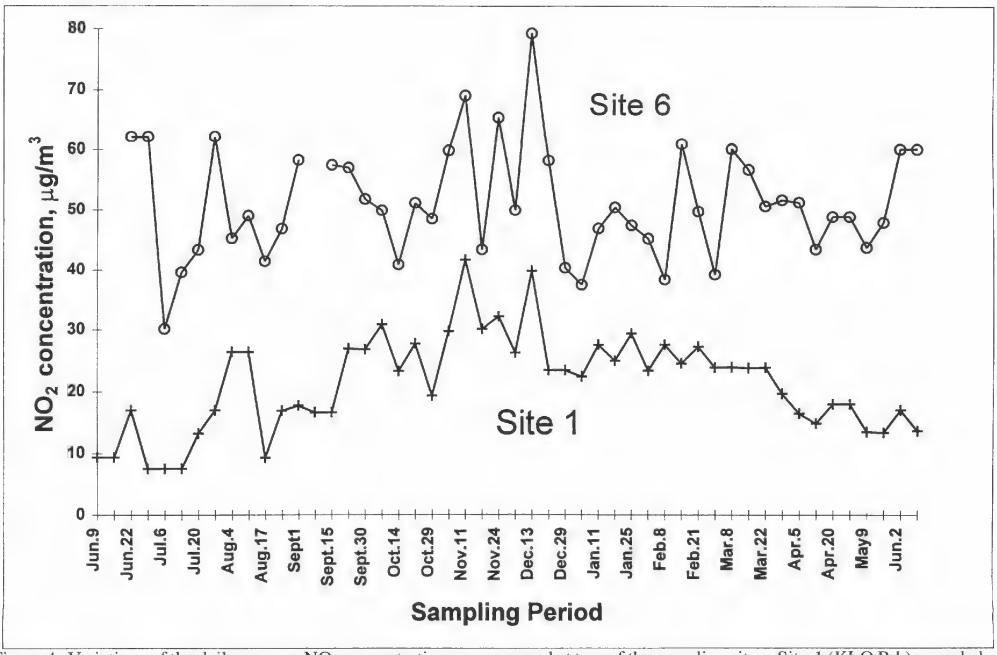

Figure 4. Variations of the daily average NO_2 concentrations as measured at two of the sampling sites. Site-1 (KLO Rd.) recorded the lowest Annual Arithmetic Mean and Site-6 (Cnr. Spall/Highway 97) the highest Annual Arithmetic Mean.

there are greater vehicle emissions due to higher traffic flow, the intense sunlight rapidly decomposes the NO_2, Equation (3). During winter, with fewer hours of sunlight, this photochemistry is not as effective and the NO_2 is not as readily removed. As indicated previously, temperature inversions in winter may also contribute to the higher winter values.

Atmospheric NO_2 also undergoes diurnal variations. Evidence for the role of NO_2 in O_3 formation is shown in Figures 5a and 5b, in which hourly data from the KLO Road monitoring station have been averaged over a one month period. Figure 5a, for August 1994, shows a typical build-up of NO_2 during the morning traffic rush (Wayne 1991; Bunce 1994). Sunlight initiates the breakdown of NO_2 and the formation of O_3. In the early afternoon, the reaction of O_3 with hydrocarbons and other species dominates the photochemistry. In the early evening, a second traffic induced buildup of NO_2 can be seen. Figure 5b, for November 1994, shows a shape similar to that for the July data, but O_3 production is impaired and the NO_2 concentration remains relatively high, due to the decrease in both sunlight intensity and available hours of sunlight.

Recommendations

Our data provide an important reference point for ambient NO_2 in interior BC. Based on these data, we make the following inferences and recommendations:

• Atmospheric NO_2 concentrations at a number of locations in the city of Kelowna indicate that this gas is not near a critical pollutant level. However, the ability for NO_2 to produce O_3, particularly during the summer months, is a major concern (Reid 1995).

• The KLO Road atmospheric monitoring station site is about 2 km from the main traffic routes and essentially measures the background concentrations of NO_2 and other gases. The measured spatial distribution of NO_2 indicates that the monitor is not ideally located if peak pollutant values are of interest. This is particularly true for O_3, as maximum concentrations for this gas are typically found down wind from the source of the primary pollutants. For example, Abbotsford, BC experiences high concentrations of O_3 generated from the NO_x/VOC gases emitted by traffic in Vancouver, BC, which is 50-70 km upwind (Concord Environmental Corporation 1990; Steyn et al. 1990).

• Continued monitoring of pollutant gases such as NO_x, CO and PM_{10}, the initiation of a spatial O_3 monitoring program, combined with a better understanding of the meteorology of the Okanagan Valley is required in order to further evaluate trends of this region's air quality. A data set of appropriate chemical and meteorological parameters could be used to develop a model suitable for predicting future air quality trends for the Okanagan airshed.

• At a local level, air quality concerns have prompted the city of Kelowna to form an Air Quality Technical Steering Committee to address pertinent issues, particularly targeting the problems of inhalable particulates, PM_{10}. The daily publication of an Air Quality Index by the BC Ministries of Environment and Health and a Venting Index by Environment Canada are recent outcomes of this Committee's deliberations. The Regional District of the Central Okanagan is currently preparing a by-law to regulate open burning and the use of wood burning appliances.

• At the Provincial level, in 1995, the BC Government introduced a "Cleaner Vehicles and Fuels - Action Plan" in which auto emission standards and gasoline quality standards, identical to those used in California, will be phased in by 2001. These control strategies, based on limiting VOC and NO_x emissions (Finlayson-Pitts and Pitts 1993; Calvert et al. 1993), are designed to prevent O_3 buildup and smog formation.

One of the authors (GRB) has recently received a grant to construct a portable O_3 monitor (Bognor and Birks 1996). It is intended to use this instrument to carry out spatial and temporal measurements of O_3, particularly downwind from Kelowna. The development of a passive diffusion tube sampler for O_3 determinations is also being investigated. An additional interest is the unexpected increase in surface concentrations of O_3 during the hours of darkness, 22:00 hours to 5:00 hours, see Figure 5b. As atmospheric O_3 is only generated in the presence of sunlight, a nighttime increase cannot be due to photochemical formation. Unusual upper atmosphere meteorological events may occasionally cause intrusion of stratospheric O_3 into the lower atmosphere. This occurs over a period of a few days when there is gross instability in the jet stream (Steyn et al. 1990) but not when there is ground level stagnant air. In 1994, the nighttime increases in O_3 concentration were observed on 25 of the 30 days in November, as well as for several days in October and December.

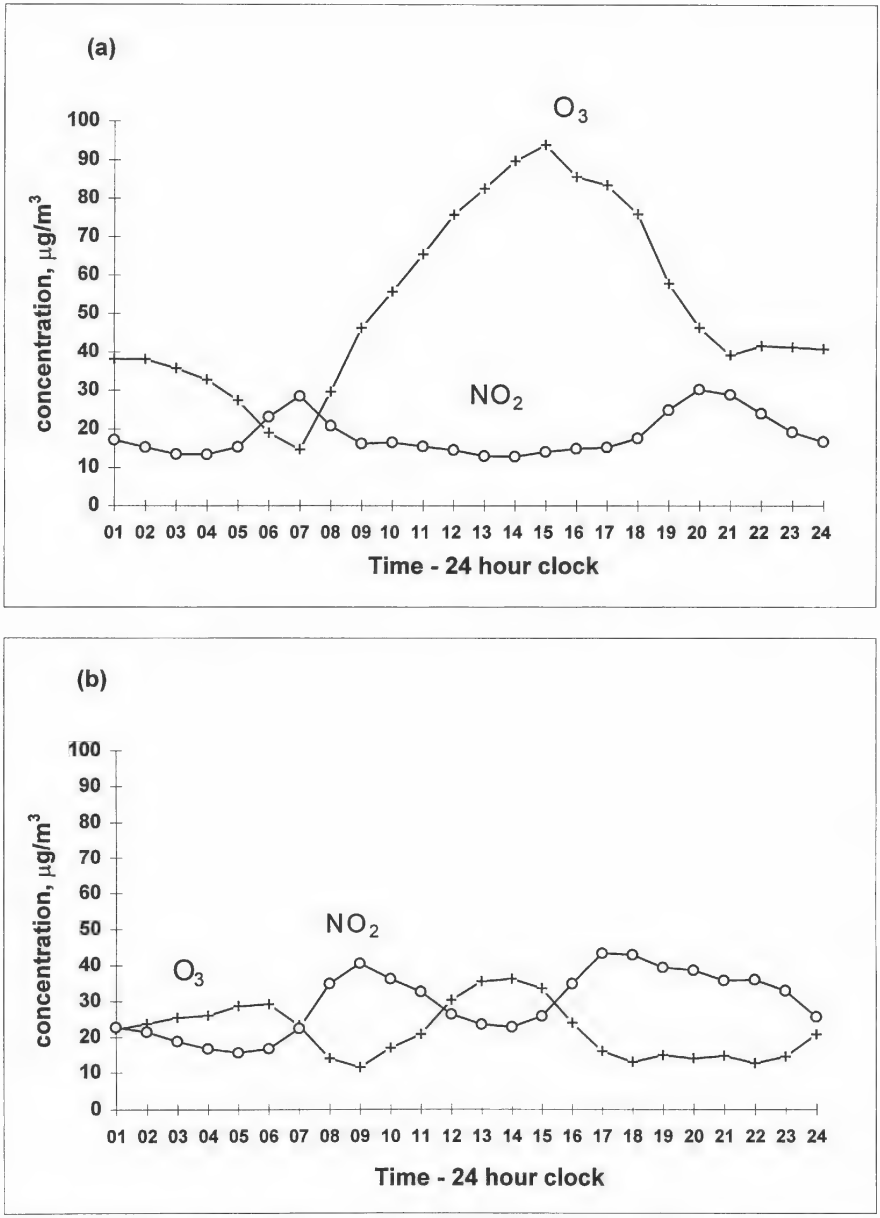

Figure 5. Hourly NO_2 (—o—o—) and O_3 (—+—+—) concentrations, averaged over an entire month, as measured by the BC Provincial Monitor (KLO Rd) for (a) August 1994 and (b) November 1994.

It is possible that daytime O_3 produced at the surface is being convectively transported aloft during daylight hours where it is not encountering sufficient hydrocarbons, sunlight and high enough temperatures for its efficient removal. This O_3 is then returned to ground level by katabatic winds during the onset of a nighttime inversion. Verification of this mechanism may be established using

the previously mentioned monitor to measure vertical profiles of O_3 concentration.

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Book Reviews

Building Knowledge-based Systems for Natural Resource Management

Daniel L. Schmoldt and H. Michael Rauscher, 1995, Chapman & Hall (Cloth, $60.00)

This book is an admirable attempt to bridge the gap between an in-depth discussion of the technology of decision support systems with the practical application of these systems to address real-world natural resource management problems. The book is divided into three sections. The first section provides a general overview of artificial intelligence techniques applicable to natural resource management. The second section deals more with issues of planning for the development of a knowledge-based application, covering prototyping strategies, knowledge acquisition, and knowledge engineering approaches. The third and most technical section gets into the nut-and-bolts of developing a knowledge-based system (KBS) using the PROLOG programming language. The three sections individually provide good overviews of their respective target areas, and taken as a whole provide a fairly comprehensive perspective on the process of developing these systems. Finally, an interesting and entertaining appendix, provided by Don Latham, is included which discusses the cultural history and "grand vision" of artificial intelligence research. Each of the sections is discussed in more detail below.

The authors provide an introduction to the broad topic of artificial intelligence (AI) and knowledge based systems development with application in the resource management domain in Chapter 1. After the usual definitions, a scenario is presented dealing with a company's decisionmaking process involved in land management, considering a variety of economic and ecological factors. This management involves keeping stockholders in the company happy, providing good stewardship of the resource, and satisfying nearby populations' concerns over timber harvests, water quality and wildlife habitat. Expertise for developing effective management options resides both within and outside the company. This sets the stage for discussions concerning how the company might incorporate a KBS into their management process, and provides an opportunity to present a general background on these systems including architectures and representational strategies.

A discussion of basic representation and control strategies for a KBS is given in Chapter 2, starting with traditional conditional (if-then) rules and then moving on to more advanced frame- and object-based representations. A detailed discussion of inferencing strategies is also presented. Additional discussion incorporates explanation generation, user interface issues, and a discussion of uncertainty analysis and propagation in rule-based systems. Taken together, these chapters provide a very complete background on the basic structures and algorithms upon which virtually all KBS's are built. The authors do a good job of balancing the need for a solid understanding of how these systems work "under the hood" with a relatively accessible explanation suitable for those who aren't computer science junkies.

The next several chapters are in many ways the most interesting and useful, and begin to separate this book from the many other KBS texts available. They delve into the planning and design process for a KBS, starting with prototype development and covering most of the important steps in the process. The authors' experience designing these systems begins to show here, as they relate the design experience from the development the Red Pine Forest Advisory System and similar systems from the natural resource management domain. The use of these examples is instructive, both for demonstrating the basic design strategies required for any generic KBS, and equally importantly for relating the strategies to tangible relationships immediately understandable by resource managers. The generally murky area of knowledge acquisition is discussed in considerable detail, and a number of well-documented approaches, along with their various strengths and weaknesses, are presented. Strategies proposed range from basic, unstructured interviews to a variety of automated machine learning techniques. Because the knowledge acquisition phase is often where KBS development efforts fail, having an extensive discussion of a complete range of approaches is particularly useful and is a valuable

contribution. The final topic presented in this section deals specifically with the design and implementation of a KBS. Here again, the authors' experience becomes evident. The frequent use of examples from resource management KBS development makes the information presented particularly easy to grasp. A number of different design strategies are reviewed, along with a discussion of currently available implementation tools.

The final section of the book deals with implementing KBS's using the PROLOG programming language. PROLOG, (PROgramming in LOGic) is a rule-based language developed originally in the early 1970's for natural language processing. Its use of logical relationships (predicates) as its fundamental language construct quickly made it a popular language for implementing artificial intelligence programs generally, and rule-base systems specifically. Widely used in Europe and Japan, it has been somewhat less popular in the United States. The non-procedural nature of PROLOG programming is both a strength and weakness; FORTRAN-style programmers often have substantial difficulty adapting to a language where programs are systems of logical relationships, rather than algorithmic control structures describing stepwise how to generate a particular result. These programmers may in fact be the best audience for this chapter. The authors do a reasonable job of presenting the basics of logic programming and how it relates to implementing a KBS. While not a substitute for a PROLOG tutorial, it is nonetheless a useful presentation for those wishing to delve into the depths of this interesting and powerful language. Finally, the authors present a PROLOG-based toolkit that may be a useful starting point for developing new KBS's. While not a complete, commercial quality package, it does have most of the basics covered, including rule representation, forward and backward chaining, uncertainty propagation and user query.

This is an excellent book for those contemplating for the first time the development of a KBS in the resource management domain. It provides excellent overviews of the basic technologies and strategies employed in KBS's, and clearly identifies the requirements and limitations of planning, designing and implementing these systems. Those involved in implementing these systems will be well served by a thorough review of the middle section dealing with the specifics of KBS planning and design. The final section dealing with implementation will be perhaps less useful to a broad audience, but those interested in logic programming and PROLOG will find useful information here. While a number of books are available discussing KBS development generally, having a text specifically related to natural resource management is a welcome addition to the fold. The authors have done a particularly impressive job covering the broad range of topics encompassed by the systems and relating them to tangible resource management applications.

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The Ecological Detective: Confronting Models with Data
Ray Hilborn and Marc Mangel, 1997, Princeton University Press (Cloth, $39.50; Paper, $19.50)

An "Ecological Detective," as defined by this rewarding monograph, is anyone who strives to interpret ecological phenomena using models. Hilborn and Mangel's detectives use their data from experiments or sampling programs to "confront" two or more competing ecological models. The winner of this competition is the model that shows the best overall goodness of fit to the data. *The Ecological Detective* explains how modern statistical and computational tools can be used to set up and referee the competition.

The concept of alternative, competing models is crucial to the authors' approach. In Chapter 2, they mount a persuasive attack on the classical paradigm of pitting a single model against an unrealistic, and hence uninformative, null hypothesis. For real scientific understanding to emerge, they believe, the contestants must include at least two plausible models and/or hypotheses. Along the way, and still in Chapter 2, Hilborn and Mangel critically review the dominant modes of modern scientific investigation, offer a taxonomy for ecological models, and clarify the relationships between "models" and "hypotheses". This chapter alone is worth the price of the book and should be required reading for graduate students in the ecological sciences. These same students, as well as their professors, should also ponder *The Ecological Detective*'s appendix, a reprinted 1890 essay in which the geologist T.C. Chamberlain eloquently warned scientists of the dangers of adopting and promoting a single, pet hypothesis.

The technical meat of the book begins in Chapter 3 with a review of the logic and algebra of probability models and distributions. The authors explain how simple probabilistic models can be added to deterministic ecological process models for the purpose of describing uncertainty and random variation over time and space, both in the process models themselves and in observational data indicative of the processes.

Three subsequent chapters explain modern, computer-intensive, methods for estimating model parameters and their confidence limits, as well as assessing model goodness-of-fit. A chapter on sums of squares gives a refreshing perspective on the goodness-of-fit assumptions underlying familiar regression and analysis of variance models. In particular, the reader is encouraged to go the extra step of computing how rapidly the error sum of squares for a fitted model increases as one varies a regression coefficient about the best-fitting value proclaimed by a statistics package. For small sample sizes and weak relationships, it can be a sobering exercise to discover that your regression slope could vary over an order of magnitude, with little worsening of the overall regression fit.

The book proceeds to a fine presentation of maximum likelihood methods. The authors do a nice job of describing the likelihood concept and of distilling likelihood equations, which are invariably large and messy, down to the terms essential for comprehension and computation. The power of the likelihood method is made clear through applications to models with nonlinearities and thresholds. We are shown how to fit multiple-parameter models, construct likelihood-based confidence intervals, and explore parameter sensitivity with likelihood profiles.

The third of these chapters explains Bayesian methods of model fitting as a natural extension of the multiple-model philosophy and of maximum likelihood. The authors argue that whenever possible we should formally incorporate knowledge from previous research into analysis of the current data set by constructing and employing prior distributions of model parameters. Although Bayesian concepts are by now familiar to most quantitative ecologists, it is hard to find an exposition of the mathematics and computation of Bayesian models that is this accessible to the nonstatistician.

To illustrate goodness-of-fit techniques, the methodology sections draw on simplified models such as those of population growth, of mark-recapture abundance estimates, and of animal emergence counts. In addition, each methodology chapter is immediately followed by a chapter laying out a single case study drawn from the authors' experiences. The case studies include modeling of incidental seabird catch in the New Zealand squid trawl fishery, models for clutch size in insect oviposition, and two management-oriented problems in population dynamics modeling,

one for Serengeti wildebeest and the other for the hake fishery off Namibia. These case studies nicely demonstrate the background knowledge, assumptions, and chains of logic that are integral to real-world model confrontations with data.

The book is rounded out by a chapter on practical aspects of fitting nonlinear models to data. Maximum likelihoods can rarely be computed in closed form, and the modeler must turn to computer search algorithms to find the best-fitting models and their parameters. This process is still as much an art as it is a science, and authors urge us not to rely on canned routines now available with many statistics and mathematics software packages. Commercial software does not yet offer likelihood profiles or Bayesian parameter estimates for arbitrary models. And even if canned routines can provide the "right" answer, our deepened understanding of model behavior and sensitivity is, in their experience, more than ample payoff for taking the trouble to write our own computer code. This chapter is full of useful tips on topics such as debugging search programs and traversing bumpy goodness-of-fit surfaces.

The Ecological Detective is not for mathematical sissies or the computationally-challenged. Hilborn and Mangel promote a hands-on approach to their material and, throughout, they present small data sets and accompanying computer algorithms in the form of pseudocode. The reader is then urged to produce working programs in languages such as BASIC or C+, to fully understand and appreciate model fitting methods. The authors claim that a year of calculus and statistics provide an adequate background, but, as every student knows, there's a world of difference between mastering (and enjoying!) mathematical coursework, and just surviving it. The former condition is essential for this book.

On the other hand, the authors appear at times to place unnecessary demands on readers' facilities for statistics and computing. I would hate to see an ecology student turn away in discouragement from this book, after trying unsuccessfully to wade into Kendall and Stuart's *Advanced Theory of Statistics* (cited for Student's t distribution) or Feller's (1968) treatise (recommended for introductory probability theory), or after discovering that it will take much more than "... a day or two" (p. 277) to learn BASIC or PASCAL.

The book has other minor flaws. It is marred by the typographic and notational errors that, sadly, we have come to expect from modern publishing. There are occasional lapses of clarity. I found the intertwined presentations of likelihood curves, likelihood ratio tests and confidence intervals to be overly terse and somewhat garbled. The case study on incidental catch of seabirds in a fishery presents two competing models for estimating catch levels, but the triumphal winner is declared after presenting only its performance, and not that of its competitor. This and other occasional gaps may, however, be turned to good use as implicit examples of the many explicit exercises the book assigns, prompting readers to "do it yourself".

These problems were few and minor. Overall, the book is engrossing and has a writing flow that carries one easily through its nearly 300 pages. It is well-indexed and crammed full of well-explained concepts and technical tips. *The Ecological Detective* is a valuable tool for quantitatively-minded ecologists trying to fit models to data, to synthesize results from multiple research efforts, or just to think critically about alternative hypotheses. I encourage you to pick up a copy, grab your programming manuals, and dig in.

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Phylogenies and the Comparative Method in Animal Behavior
Emilia P. Martins, editor, 1996, Oxford University Press ($49.95)

Comparisons among extant taxa offer ethologists excellent opportunities to both generate and test hypotheses concerning behavioral function and evolution, in the absence of a fossil record. The so-called comparative method has a long history, and was clearly important to Darwin as he developed his theories of natural and sexual selection. However, beginning in the 1970s the comparative method underwent a revolution as it became clear that comparisons among taxa must be considered in an explicitly phylogenetic context.

The initial impetus for thinking phylogenetically was the need to preserve statistical independence when comparing data derived from different species. Thanks to ancestor-descendant relationships, species cannot be considered as truly independent data points in a statistical analysis. Secondly, ethologists realized that they could better understand the evolutionary history of behavior patterns by 'mapping' the distribution of their characters onto independent phylogenetic hypotheses. Using techniques provided by that branch of systematics known as cladistics, ethologists sought to separate ancestral from derived behavior patterns, and to distinguish similarities due to common descent from those due to convergence. Even the knotty problem of how to diagnose adaptations from fortuitous effects became easier to resolve with the advent of thinking phylogenetically.

Today, formal phylogenetic analyses are incorporated into many comparative studies in ethology. And those that lack formal analyses usually acknowledge that they would be informative.

A huge primary literature has evolved, much of it rather technical and quite statistical. As *Phylogenies and the Comparative Method in Animal Behavior* clearly shows, thinking phylogenetically has a great deal to offer those of us interested in ultimate questions about animal behavior.

This book emerged from a symposium organized by the editor for the 1994 annual meeting of the Animal Behavior Society (held at the University of Washington). Not all of the original symposium attendees are authors, and not all authors were attendees. Twenty three biologists with differing conceptual and taxonomic interests have written 13 chapters to meet the editor's stated goals of review, synthesis and prospectus. All chapters provide ample references to the primary literature, the book's index is adequate, and typos are few and inconsequential. The result is a fine, critical overview of what I will call the science of *phyloethology*.

Anyone who picks up this volume hoping to find a 'user's manual' or 'cook book' approach to phyloethology will be somewhat disappointed. As all of the authors make clear (but especially forcefully in four chapters grouped under the heading *Taking Phylogenies Into Account*), there is *no* single (or simple) algorithm in phyloethology. The authors do an excellent job of discussing the varied conceptual and theoretical issues that underlie the different analytical methods that are available. Many of these issues can be put in the form of a set of questions that every prospective investigator should ask of her system. Perhaps the most important of these questions are the following. What model of evolutionary change do I think is most appropriate (e.g., drift versus selection)? Will my data consist of continuous and/or discrete characters? How robust is my phylogenetic hypothesis (assuming that I have one)? And does it suggest a branching, tree-like pattern or something more reticulate and bush-like (perhaps implying contemporary gene flow, as may exist among conspecific populations)? Answers to questions like these are necessary before deciding on which comparative methodology is most appropriate.

A second set of chapters, under the heading *Comparisons of Behavioral and Morphological Evolution*, uses phylogenies to explore the extent to which behavior patterns evolve with the same mode and tempo as other phenotypic characters, especially morphological and life historical ones. Most of the authors discuss the old chestnut that behavior patterns are especially plastic, and easily evolve in different directions over short periods of time. One message that I take away from these chapters is that, although some behavioral characters may show high levels of convergent or parallel evolution (or homoplasy), others don't. Thus to simply say that behavior is 'plastic' is to make a *very* broad generalization! Furthermore,

those behavior patterns that are not especially homoplasious may be just as useful as, say, morphological characters for estimating phylogenetic relationships. It is the widespread assumption that behavior patterns are especially homoplasious that has led to their growing disuse as phylogenetically-informative characters.

Comparative Studies in Animal Behavior is the heading for the third set of chapters in this book. Considering taxa as different as eusocial insects and primates, these chapters provide some nice examples of phyloethological methods in action (of course, 'real' data are scattered throughout the book). If there's a single message running through these diverse studies, it is surely that a taxon's evolutionary history can greatly influence the way it behaves in contemporary environments. Simply put, history matters!

These 11 chapters are bounded by an Introduction and a Conclusion. Both of these are certainly enthusiastic about phyloethology, but with caveats. Most importantly, they stress that phyloethology is but one tool for addressing ultimate questions in animal behavior. It is a tool that likely will be most powerful when coupled with classical experimental approaches and mathematical simulation/modelling.

Who is the audience for this book? That it is crucial reading for and should be owned by every ethologist interested in comparing the behavior of different taxa goes without saying. But it should also be read by any other '-ologist' who believes that, when applied appropriately, thinking phylogenetically is a crucial component of modern organismal biology. Martins' volume clearly belongs on any bookshelf that also houses Brooks and McLennan's *Phylogeny, Ecology, and Behavior* (1991, University of Chicago Press), Harvey and Pagel's *The Comparative Method in Evolutionary Biology* (1991, Oxford University Press), and Harvey et al.'s *New Uses for New Phylogenies* (1996, Oxford University Press).

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Foundations of Animal Behavior: Classic Papers with Commentaries
Lynne D. Houck, Lee C. Drickamer, editors, 1996
(Cloth, $95.00; Paper, $34.95)

Few people appreciate where their ideas and beliefs originate, be these political, social, or intellectual. *Foundations of Animal Behavior* reprints 44 original papers that are windows into the intellectual antecedents of nearly all current work in this field, plus six commentaries by eight authors that place the papers into historical context. Practising animal behaviorists and students will find delving into the ontogeny of the field as rewarding as studying the ontogeny of a behavior itself, one of several complimentary approaches that lead to a full appreciation of the issues involved. While students need not recapitulate all aspects of the field's development in their own thinking, most will benefit by reading original works that contribute to their internalized perspective.

The 843-page publication was sponsored by the Animal Behavior Society. An eight member committee representing the spectrum of sub-disciplines debated and pruned a list of over 200 papers initially suggested for inclusion. Necessary, though not sufficient conditions for inclusion appear to have been originality, and, in most cases, clarity of thought or outcome. The committee explicitly looked for "major impact on subsequent research" or "the impact of key works on current research paradigms", with hindsight as a guide. These criteria resulted in a concentration on mid-twentieth century papers, with only five selections from prior to the Second World War, and 39 papers published between 1941 and 1974. The cutoff date is a year after the awarding of the Nobel prize for medicine to Lorenz, Tinbergen, and von Frisch, an event that gave widespread recognition to the emergence of a new science, and a period that coincides with the rise of behavioral ecology as a strong subdiscipline within animal behavior.

Few of the papers have been reprinted previously. While most are relatively lengthy discussions of broad issues, at least a third of the papers that survived the stringent selection process are basically single-species studies directly addressing relatively narrow questions. The take-home lesson is that timely and clearly presented "case studies" can transcend their subdiscipline become broadly influential.

Six sections cover "Historical Origins", from Darwin through World War Two; "The Emerging Science", dealing with goals, approaches, and methods; "Development and Learning", including genetic influences; "Neural and Hormonal Mechanisms of Behavior"; "Sensory Processes, Orientation, and Communication"; and "Evolution of Behavior". Each section is preceded by a commentary.

Commenting on "Historical Origins", Bennet Galef, Jr., emphasizes the late 19th and early 20th century change from discussing animal behavior in terms of animal minds and intelligence, based on anecdotes and anthropomorphism, to a narrower, experimental, behaviorist approach that rejected the value of anecdotes and speculation about animal cognition, particularly in North America (e.g., Watson). He views this shift as a necessary reaction to the predominant Victorian approach, of which he considers Darwin an exception, and concludes by noting that a more balanced approach is taken today, with ad hoc observations frequently providing legitimate inspiration for formal study.

I question the inclusion of an excerpt by Romanes, who wrote volumes on "Animal Intelligence" in 1882. I admit to being totally ignorant of Romanes work, but wish I still were. Galef includes the selection as a foil, representative of an uncritical approach that may have impeded the development of Animal Behavior as a science for decades. This may be so, but its reprinting here seems to violate the selection criteria stated above.

Lee Drickamer and Charles Snowdon's section "The Emerging Science" emphasizes the constructive exchange and cross fertilization between European an North American approaches during the mid-century, rather than concentrating on differences between schools of thought. Niko Tinbergen's famous 1963 essay "On Aims and Methods of Ethology", outlining a four approaches to the subject: physiological "causation", interactions between genes and environment during development, current survival value ("function"), and evolutionary history stands up to modern scrutiny. The remainder of their section considers

how to define and sample behavior (Barlow, Slater, Altmann), followed by papers considering more evolutionary questions (e.g., Baerends, Hodos and Campbell).

The eternal dissection of genetic, environmental, and interactive components controlling development is covered in Charles Snowdon's section on Development and Learning. Selections include classic demonstrations of simple genetic manipulations of behavior (e.g., Bastock's *Drosophila*, Bentley and Hoy's crickets), papers demonstrating species' predispositions to learn particular tasks (Garcia and Koelling), and Harlow and Zimmermann's 1959 study of mother-infant relationships. Snowdon argues that this latter study substantially affected our own child-rearing practices.

Elizabeth Adkins-Regan introduces papers on physiological mechanisms. The selections concentrate on the central vs. peripheral control of behavior, where ethologists consistently argued against a simple stimulus-response paradigm (e.g., Tinbergen, Ashoff); the effects of social behavior on internal physiology (e.g., Lehrman's ring doves); other papers on hormonal and neuroethology, the latter emphasizing an integration of neurobiology with whole-animal behavior; and conclude with papers addressing motivation (e.g., Dethier and Bodenstein's blowflies, Hinde's ideas), a long-time central concept that has disappeared in much of the discipline. Adkins-Regan closes her introduction by asking whether completely replacing "motivation and drive" with "information processing, decision making, behavioral rules such as foraging rules" is wholly warranted.

A section on the *Umwelt* of animals— their sensory, orientation and communication processes— is introduced by Fred Dyer and Jane Brockmann. The realization that other species of animals perceive environmental and social features that we are blind to (e.g. Griffin's bats, Hasler's salmon), and transmit and respond to signals we do not perceive, had a "liberating influence" on behavioral study and stimulated much fundamental neurophysiological study. The most outstanding example, for me, is Edward Wilson and William Bossert's paper on chemical communication, which presents frameworks for considering how and why information might be encoded, perceived, and utilized in a modality we experience in such a limited fashion. As the commentators point out, considering Peter Marler's thoughtful analysis of signalling structure with respect to motivation provides a counterpoint to the game theory approach towards analysing communication in vogue today.

The final section, on Evolution of Behavior, introduced by Stevan Arnold and Jane Brockmann, presents papers emphasizing phylogenetic history, on the one hand (e.g. Lorenz, Howard Evans), and current selective value ("adaptation"), on the other. These selections highlight comparative (Cullen's kittiwakes), experimental (Tinbergen et al.'s study of egg shell removal by black-headed gulls), and various modelling approaches (W.D. Hamilton, Orians, Trivers, Maynard Smith and Price) towards studying adaptation.

In their introduction, the editors point out that recent attempts to enforce copywrite laws make putting together a set of readings for a university course more of a chore than formerly, enhancing the prospect that such a market exists for this book. However, the production of the volume was clearly a labor of respect, if not love. Neither editors nor commentators will get rich from sales of this book, even if it sells well. All author and editor royalties will be donated to the Animal Behavior Society's fund for student research. Today's students, in addition to utilizing the knowledge and concepts handed down by the reprinted authors, may thus obtain a modest financial benefit from the work of their predecessors.

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The Rain Forests of Home: Profile of a North American Bioregion

Peter K. Schoonmaker, Bettina von Hagen and Edward C. Wolf, eds., 1997, Island Press, Washington, D.C. ($27.00)

In the early 1970s, when I was moving to southern Arizona, I was lucky enough to encounter Roger Dunbier's masterpiece "*The Sonoran Desert: Its Geography, Economy, and People.*" With succinct but flowing prose and well chosen facts, Dunbier described this distinctive region's physical geography (landforms, climate, soils, water, vegetation), its social evolution from earliest Amerinds throught Spanish and Anglo-American settlements to the present day, the development of regional resources (mining, farming, water resources) and economic structures, and the roles played by past and current political actions. Woven together very carefully, the chapters of *The Sonoran Desert* provided a superb means for newcomers and natives alike to understand the interactions of physical, economic and social patterns and constraints which characterize that arid region. As one of those newcomers, I found it exceedingly valuable.

Like *The Sonoran Desert*, the new volume from Island Press entitled "*The Rain Forests of Home: Profile of a North American Bioregion*" will be invaluable to all those who possess an interest in understanding, and a bit (or a lot!) of ignorance concerning, the natural and human patterns and structures which characterize the unique forested region we know as the Pacific Northwest Coast. Edited by Peter K. Schoonmaker, Bettina von Hagen and Edward C. Wolf, *The Rain Forests of Home* begins with the physical geography which constrains and supports life here: the oceans and their circulation (David K. Salmon); the resulting regional climate (Kelly Redmond and George Taylor); and, the role of landforms and geology in defining regional climate and landscape characteristics (David R. Montgomery). As Chapters 1, 2 and 3, respectively, these three reviews cover the first 68 pages and alone may be worth the price of the book; they are very well written and carefully coordinated.

Thoughtful reviews then describe natural systems which follow from, and derive their uniqueness from, the processes examined in the first three chapters. The nature of and variability among coastal streams and rivers is discussed in Chapter 6 (Robert J. Naiman and Eric C. Anderson). The processes which control and characterize land-water interfaces such as seashores, estuaries, and stream floodplains appear in Chapter 7 (Charles A. Simenstad, Megan Dethier, Colin Levings and Douglas Hay). The natural vegetation (Paul Alaback and Jim Pojar) and vertebrate communities (Fred C. Bunnell and Anne C. Chan-McLeod) typical of the terrestrial environments are reviewed in Chapters 4 and 5. Coupled with the Pacific salmon life history (Chapter 8 by Willa Nehlsen and James A. Lichatowich), the ecological origin and development of the region since the continental glaciers began retreating some 15,000 years ago (Chapter 9 by Richard J. Hebda and Cathy Whitlock), and the human habitation before the region was "discovered" by Europeans (Chapter 10 by Wayne Shuttles and Kenneth Ames), this group of chapters forms a relatively comprehensive and very informative review of the natural systems which both constrain and sustain human activities in our coastal forests.

The remaining chapters deal with human activities and approaches which have resulted because of and despite the limitations and characteristics of the natural systems which comprise the coastal forest region. An illuminating chapter (11, by Nancy J. Turner) describes "Traditional Ecological Knowledge," that is, the ecological information and principles understood by First Nations peoples. Another chapter (12, by William G. Robbins) deals with the global and regional cultural context of European transformation of the "great raincoast," a very different vision from that of native Amricans, based instead on capitalism, eminent domain and world trade. A third chapter (13 by Hans D. Radtke, Shannon W. Davis, Rebecca L. Johnson and Kreg Lindberg) examines the recent evolution of the coastal economy, that is, the decline of resources which support forestry and fishing. A fourth chapter in the group (14 by Ken Lertzman, Tom Spies and Fred Swanson) reviews the recent applications of ecological knowledge on natural disturbance (fire, pests, disease, flood, slides) to a more natural management of forest resources.

As a whole, this group of chapters integrates the human element into the coastal forests, both in the past and the present, as a means to predict

future trends, problems and solutions in the region. The final chapter (15, by the editors) attempts to provide this synthesis, as well as developing "A Vision for Conservation-Based Development in the Rain Forests of Home." The attempt appears to be eminently successful; it integrates specific characteristics of the history and processes of the region's physical, natural and human systems, which were elucidated in the earlier chapters, with the author's and editor's considerable excitement about a future in which ecologic, economic and cultural needs are met simultaneously in truly win-win situations.

Providing significant support for this synthesis is a unique group of sections in the book I have not mentioned; these are "Concepts in Action," sets of 4-8 essays of a few pages each, describing specific actions taken by groups working together to solve regional resource problems. The sections deal with restoration and management of ecosystems, initiatives to enhance health of forestry and fisheries, attempts at conservation-based development, and new approaches to decision-making and environmental understanding. These essays provide a superb sense of what can be accomplished when ordinary (and extraordinary) citizens are willing to work toward the goals the book represents, and to open their minds to the ideas and concepts of diverse others seeking the same goals. The essays also provide excellent food for thought, and generate can-do optimism, among those who perceive a need to enhance environmental quality but are overwhelmed by the apparent enormity of the task.

This book can be invaluable for many of the region's inhabitants, including newcomers seeking familiarity with the region, citizens wishing to exercise their duties, business people wishing to conduct commerce in environmentally-responsible ways, and the scientifically-minded who need the environmental background to underpin more specialized activities. I recommend it without reservation.

—Allen M. Solomon
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Creating a Forestry for the 21st Century. The Science of Ecosystem Management
Kathryn A. Kohm and Jerry F. Franklin, eds., 1997, Island Press, Washington, D.C. 475 pages.

This book evolved from the 1993 conference in Portland, Oregon, "Creating a Forestry for the 21st Century." It contains twenty-nine chapters authored by 52 contributors representing viewpoints of ecologists, silviculturists, forest analysts, social scientists and others. The title and subtitle purport to be much more definitive and concrete than are either the stated intent, "... a conversation about the future of forestry" (p. 1), or the contents, which are more conceptual, conjectural and expositions of working hypotheses than "a forestry" or "the science". However, as the editors state, this book is a beginning in a process. Assuming that process to be an open, evolutionary dialogue about a range of forest management possibilities for the 21st century, this book will make a major contribution in the ongoing process by establishing in one volume the bases for considering ecosystem management. In their introduction editors Kohm and Franklin write, This is "... the beginning of the conversation." I think it would be reasonable to expect that a more comprehensive "conversation" about forestry for the current and next generation would include voices of significant, thoughtful representatives of private forest land owners and of corporate forest industries; and, of those involved in academic forestry and in public forest land management who still believe that intensively managed forests will be essential to contribute to society's demands for wood products.

The foreword sets the constraints and limitations of the book in that it, and most of the book, focus almost exclusively on the setting and policies for federally-managed public lands, as though forestry on industrial, private, state, native American and other lands were of no consequence for forestry. In my view, the book does a good job of laying out the scientific basis for the hypotheses of ecosystem management, but only in a few chapters do authors provide much basis for developing operational context for forestry on the land.

Of fifty-two contributors, many are federal and academic ecology researchers from the Northwest, none with direct forest management responsibilities. Significantly, none of the contributors are from British Columbia, a significant source of leadership in the practical ecological classifications of forested lands and of much excellent development of understanding of forest ecosystems in relation to management. If "forestry" is the science and art of managing forest lands for the desires and benefits of humans, this volume seriously underrepresents the "managing" aspect of the profession. Surely forestry scientist and management colleagues from Canada, Scandinavia and elsewhere and forest managers provide significant voices that should be engaged in conversations about future forestry, whether it is for the Pacific Northwest of the USA, or for the continent or world.

The book is well-organized into five sections, each with a good introduction: "Ecological Processes and Principles"; "Silvicultural Systems and Management Concerns"; "Approaches to Management at Larger Spatial Scales"; "Forest Economics: Products and Policies"; and "Institutions in Transition". There is a reasonable distribution of space given to each of these sections, with, perhaps not enough devoted to economics and a bit much to institutions, a topic which has the least substantial, concrete treatment. Missing from the economics section is substantial treatment of comparisons of systems for and costs of obtaining wood products from traditional versus ecosystem-management forestry. And, surprisingly, there is no coherent treatment of mpacts on forest products-based communities of implementing ecosystem-management forestry.

In the chapter, "Forest Stand Structure, Composition and Function" Tom Spies discusses forest structure and function in lucid, straightforward fashion. He clearly separates well-established knowledge from working hypotheses, and emphasizes the need for distinction between forests managed for all ecosystem values and those managed primarily for forest products. He states that where objectives call for maintenance for many forest values "... the challenge to management is to determine the mix ... of... stand conditions and disturbance regimes that will meet the diversity of objectives. ... Prudence calls for an adaptive ecosystematic approach that spreads environmental

risks across management strategies ranging from reserves to restoration to intensive plantations." Spies's treatment of forest ecology is the best, least speculative piece on ecology, and contains none of the "organism/hypothesis-affinity" that bedevils some other authors.

In "The Biological Landscape", Malcolm Hunter urges us to take the "landscape view" as though we had wings and could fly over and discuss the patterns that exist and are imposed on our forested landscapes. While focusing on animal ecology, Hunter advocates a "triad" model of land uses that include: ecological reserves with no resource extractions; seminatural ecosystems managed for multiple uses; and "agriculture-style" ecosystems intensively managed for commodity production. This triad idea would have been an excellent launching point for someone to expand on the potentials for managing landscapes with a mixture of intensities of uses, landscapes like those in parts of Sweden and Finland. Hunter cites the example of landscapes in which wood can be grown in plantations three times as fast as in managed seminatural forests: harvesting wood from seminatural forests could fragment three times as much landscape as wood production in plantations. Managing a matrix of mixtures of land use intensities seems preferable to Hunter than other alternatives. Stan Gregory, in discussing the broad considerations and specifics of riparian zone management, states "... the wide array of land ownerships, ecosystem types, and changing demographic patterns will translate into complex goals and management practices ... within the region." This recognizes the necessity of considering ecosystem management in the context of the mosaics of ownerships of and objectives for forests on the land.

In "Silvicultural Systems and Management Concerns" authors of three chapters discuss alternative silvicultural systems for ecosystem management, but avoid making explicit comparisons of proposed systems with traditional clearcut harvest, seed-tree and shelterwood systems. Unfortunately, there is no discussion of recent continental or Scandinavian European experiences with silviculture systems, some of which represent intriguing alternatives. Robert Curtis's chapter, "The role of extended rotations" is the most coherent, concise, "action-oriented" chapter. Curtis discusses the considerable merits, and perplexing limitations, of long rotations (100+ years) with thinnings, options that are very attractive if the transition to them could be achieved while maintaining wood supplies and economic forestry.

In "Approaches to Management at Larger Spatial Scales" especially relevant are the discussion of landscape analysis and design by Diaz and Bell, and the concrete example of spatial planning with ecological constraints by Sessions et al.. Chapters on economics by Haynes and Weigand and on changes in wood products by Whittenbury contain, in my view, two of the clearest, most insightful and straightforward discussions in the book. Each calls for hard-nosed evaluations of the implications of ecosystem management for forest-based economies and wood products manufacturing, and poses questions managers must face as they consider major changes in products to be derived from future forests.

"Institutions in Transition" provides discussions, some useful with examples, some less useful and more theoretical, of the legal, policy and organizational situations and constraints in traditional forestry, and of coalitions evolving in locales where non-traditional approaches to forest management issues are being pursued. These chapters present some useful springboards for considering changes in institutional arrangements likely to be needed for effective ecosystem management-based forestry, where it might be feasible on a significant scale. This section would have benefited from a chapter on transitions in traditional forest products-based communities.

The book is attractive and well-formatted in a durable-appearing, high quality flexible binding that keeps cost down. There is an interesting color photo section illustrating many of the key features of ecosystem management. Literature cited sections for each chapter appear very useful for those choosing to read further. I found a very few minor typographical/editing errors. A well-produced volume.

The editors write, "From the knowledge gleaned from forest ecosystem and landscape research in recent decades"... we are reminded of the tentative state of our knowledge and the iterative nature of learning. "For skeptics, we hope this book will provide a compelling case for thinking creatively beyond the bounds of traditional forest resource management." For those truly interested in advancing forestry and willing to take the time to read and thoughtfully consider this book, there will be wonderful challenges for creative thinking beyond

traditional bounds, and for those willing to take actions in response to the challenges of the book, there will be exciting ideas to support continuing advances in forestry towards a broader sound ecological basis in keeping with evolving knowledge of forested systems, human uses and management.

—James R. Boyle
Professor of Forestry and Soil Ecology
Forest Resources Department
College of Forestry
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_____. 1970b. Populations of the yellow pine chipmunk, *Eutamius amoenus.* Amer. Midl. Nat. 83:472-488.

Ceska, A., and H. Romer. 1971. A computer program for identifying species group. Vegetatio 20:48-73.

Grizze, J. E., C. F. Starmer, and G. G. Kuch. 1969. Analysis of categorical data by linear models. Biometrics 25:489-504.

Monographs or books

Jennings, H. S. 1906. Behavior of the Lower Organisms. Columbia University Press, New York.

Papers in proceedings or symposia

Ryland, J. S. 1975. Parameters of the lophophore in relation to population structure in a bryozoan community. *In* H. Barnes (ed.) Proc. 9th Eur. Mar. Biol. Symp., Aberdeen University Press, Aberdeen. Pp. 363-393.

Theses, dissertations, personal communications, and articles in press

Donald, D. B. 1971. The limnology of the plankton of three temporary pons in Alberta. University of Calgary, Calgary. M.S. Thesis.

Wiser, H. C. 1961. Decomposition and homogeneity of continua on 2-manifolds. University of Utah, Salt Lake City. Ph.D. Dissertation.

Danwiddie, P. W. In Press. Dichotomous key to conifer foliage in the Pacific Northwest. Northw. Sci.

Technical Bulletins

Daubenmire, R., and J. B. Daubenmire. 1968. Forest vegetation of eastern Washington and northern Idaho. Wash. Agric. Exp. Sta. Tech. Bull. 60. Washington State University. 210 p.

Goodwin, J. G., Jr., and C. R. Hungerford. 1979. Rodent population densities in pine forests. USDA For. Serv. Res. Pap. RM-214. Rocky Mtn. For. Range Exp. Sta., Fort Collins, Colorado. 39 p.

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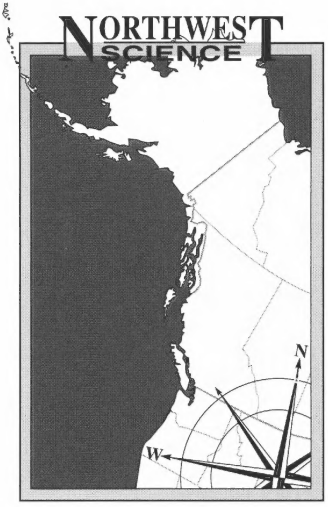

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